QUANTITY AND QUALITY OF FRESHWATER REARING HABITAT IN RELATION TO JUVENILE PACIFIC SALMON ABUNDANCE IN THE KULUKAK RIVER, ALASKA

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Abstract

Monitoring of freshwater habitat and its influence on stream-rearing fish is essential for recognizing and mitigating the impacts of human- and climate-induced changes. For the purposes of developing a monitoring program in the U.S. Fish and Wildlife Service Togiak National Wildlife Refuge, densities and habitat relationships of juvenile coho salmon *Oncorhynchus kisutch* and sockeye salmon *O. nerka* were estimated in two tributaries of the Kulukak River, Alaska, in July 2010. Multiple-pass depletion electrofishing was used to estimate density in a random sample of habitat units belonging to one of four categorical habitat classes. Regression methods were also used to quantify the physical habitat associations of juvenile coho and sockeye salmon density in the study areas. Densities of juvenile coho and sockeye salmon ranged from 0.22 fish·m^{-2} in West Fork riffles and 0.05 fish·m^{-2} East Fork riffles to 2.22 fish·m^{-2} and 1.32 fish·m^{-2} in East Fork eddy drop zones (EDZ), respectively. The largest proportions of freshwater habitat were comprised of run (71%) and EDZ habitats (44%) in the East Fork and West Fork, respectively. Regression coefficients for coho and sockeye salmon densities were positive with respect to proportional areas of in-stream overhanging vegetation (0.78 and 0.74, respectively), large wood (0.99 and 0.97, respectively), and undercut banks (0.99 and 0.02, respectively). Conversely, coho and sockeye salmon density was negatively related to depth (-1.45 and -0.52, respectively) and velocity (-2.45 and -1.67, respectively). Although substrate size was negatively related to sockeye salmon density (-0.40), this variable had a weak positive relationship with coho salmon density (0.08). These findings suggest that EDZ habitats are important for juvenile coho and sockeye salmon during summer rearing and in-stream cover is an essential component of these rearing habitats.

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Introduction

The dynamics of Pacific salmon *Oncorhynchus* spp., both at the individual and population level, are sensitive to changes in freshwater rearing habitat quality and quantity. For stream-rearing salmon, such as coho salmon *O. kisutch* and sockeye salmon *O. nerka*, biological production of smolts is strongly tied to growth and survival during the freshwater rearing stage (Mason 1976; Kocik and Ferreri 1998; Quinn 2005). Survival of fry to smolt outmigration has been linked to several freshwater habitat factors, including the quantity of available overwintering and summer rearing habitat and the quality of those habitats in their capacity for providing sufficient forage prey and protection from predators (Nickelson et al. 1992; Quinn and Peterson 1996; Nickelson and Lawson 1998). Insufficient quantities of suitable freshwater habitat leads to lower production of juvenile salmon and diminished returns of spawning adults (Quinn and Peterson 1996; Pajak 2000). For this reason, it is critical to understand the relationships between Pacific salmon and their freshwater rearing habitats.

Direct correlations between juvenile salmon abundance and physical habitat quality are well established in the literature (e.g., Rosenfeld et al. 2000; Anderson and Hetrick 2004; Nemeth et al. 2004). In-stream cover, including large woody debris (LWD), overhanging vegetation (OHV), and undercut banks (UCB), are important structural components of high quality rearing habitats for juvenile salmon (Shirvell 1990; Crook and Robertson 1999; Inoue and Nakano 2001). Large woody debris and UCB provide refuge from avian and fish predators and high water velocities (Murphy and Hall 1981; Welsh et al. 2001). For example, analyses by Mellina and Hinch (2009) showed that juvenile coho salmon abundances were positively related to the amount of LWD in pool habitats in southeastern Alaska streams. Providing shade and thermal refuge and visual isolation from avian predators, as well as connecting riparian and stream environments for influx of terrestrial invertebrate prey are important functions of OHV (Butler and Hawthorne 1968; Wipfli 1997).

In addition to in-stream cover, hydraulic variables such as water depth, velocity, and substrate composition also affect salmon abundance. Observations by Fausch (1993)

indicated that juvenile coho salmon preferred habitats with velocity refuges, suggesting that fish avoid high velocities when possible. Juvenile salmon have also been shown to occupy shallow depths when cover is present and to move to the middle of the water column in the absence of cover and presence of interspecific competitors (Dolloff and Reeves 1990; Bugert et al. 1991). Coarse substrates and low levels of suspended sediment have been shown to be positively related to salmon abundance (Crouse et al. 1981; Bisson et al. 1988; McMahon and Hartman 1989; Suttle et al. 2004; Bolliet et al. 2005). For instance, May and Lee (2004) showed that juvenile salmon abundance decreased by 59% over one summer in gravel-bed pools, and attributed this change to insufficient hyporheic flow caused by high levels of deposited sediments in the stream bed. Healthy rearing habitats are essential for sustaining freshwater salmon production; however, the quality of those habitats is often directly linked to local climatic regimes and beyond the control of management.

At northern latitudes, climate shifts negatively impact freshwater rearing habitat and freshwater salmon production. Climate shifts projected for subarctic coastal ecosystems, such as the salmon-producing rivers of Bristol Bay, Alaska, include increased winter temperatures and rainfall, reduced summer precipitation, drying of coastal wetlands, and reductions in groundwater availability (Rouse et al. 1997; Wigley 1999; Poff et al. 2002; Walsh et al. 2005). For these ecosystems, the outcome will be higher water temperatures and greater habitat availability during winter, but lower water levels and reduced habitat quantity during summer months (Bryant 2009). Under this scenario, increased juvenile salmon mortality due to habitat fragmentation and stranding is probable (Nickelson et al. 1992; Battin et al. 2007). As habitat quantity decreases, juvenile salmon will become concentrated in suitable habitats and experience increased competition and decreased individual prey intake and growth (Nickelson et al 1992; Rosenfeld et al. 2000).

While the relationships between climate, Pacific salmon abundance, and habitat quantity are relatively straight forward, climate effects upon abundance-habitat quality relationships can be highly complex. For instance, Poff et al. (2002) suggest that northern

latitude streams will experience fewer or weaker spring flood events, which are necessary for moving and depositing large wood in the stream channel (Poff et al. 1997). Large wood and boulders are important refuges for fish and are essential for formation of off-channel pool habitats (Hauer et al. 1999). With warmer water temperatures and fewer spring floods, species associated with stream bank stability such as cottonwood *Populus* spp. and alder *Alnus* spp. are predicted to dominate sedges *Carex* spp. and grasses in riparian plant communities (Auble and Scott 1998; Merritt et al. 2010; Ström et al. 2012). This shift could translate into increased UCB and decreased OHV cover available for stream-rearing fishes. The combined effects of UCB, OHV, in-stream structure, and pool formation on fish-habitat relationships are difficult to predict. As a result, it is imperative that freshwater habitat and fish abundance data be collected now for assessment of climate effects in the future.

The freshwater ecosystems in southwestern Alaska and the largest wild runs of sockeye salmon in the world are likely to be impacted by changing climate. These fish, and other species of Pacific salmon, are important commercial, sportfish, and subsistence resources in Bristol Bay, Alaska. Subsistence fishing is a way of fortifying tradition and culture, as well as ensuring food security among Alaska Natives and residents of Bristol Bay communities in southwestern Alaska. These stocks also support significant commercial fisheries, which provide income and economic stability for the region (five Pacific salmon species; average annual value since 1988 = $124.8 million U.S.; Jones et al. 2008). Sport fisheries and guide services host thousands of visiting anglers every year, fostering tourism and stimulating local economies (Alaska Department of Fish and Game [ADFG], unpublished data). To provide the greatest benefit to the users of Bristol Bay's salmon resources while ensuring their persistence for future generations, is it imperative that monitoring and conservation focus on the habitats the fish depend on.

Bristol Bay salmon stocks have been recognized as one of the most productive and sustainably managed fisheries in the world (Hilborn et al. 2003). This is believed to be a result of conservative commercial harvests, favorable climatic conditions, and high productivity of several stocks throughout the region (Hare et al. 1999). High net

productivity of Bristol Bay salmon has been attributed to the complex suite of life-history traits represented by distinct spawning stocks, which number in the hundreds in some rivers (Taylor 1991; Dittman and Quinn 1996). This diversity has rendered the metapopulation highly resilient to interannual changes in climate, harvest, and natural mortality. In other words, Bristol Bay salmon stocks are phenotypically adapted to their natal streams, and the variability between those freshwater habitats, both spatial and temporal, allow a stock to flourish in some years and diminish in others while maintaining net productivity of all stocks (Wood 1995; Hilborn et al. 2003). Maintaining the phenotypic diversity and population stability of Bristol Bay salmon by monitoring and conserving their freshwater habitats will give salmon stocks an advantage in adapting to future climate changes.

The most significant obstacle to monitoring salmon habitat is the field work required to obtain data that are large scale and of sufficient resolution to be useful for management purposes (Fausch et al. 2002). Traditional habitat assessment methods are often subjective, expensive, and time-intensive (Rosenfeld 2003). Solutions to these problems have been proposed; for example, the basinwide visual estimation technique (BVET; Dolloff et al. 1993) uses classification schemes to categorize distinct areas of homogenous flow, substrate, gradient, and streambed morphology. These areas, defined as habitat units, are visually estimated for length, width, and qualitative variables, and are sampled systematically according to BVET protocol. Although this method is cost-effective and reasonably accurate relative to methods that involve direct measurement of habitat units, it still requires walking the entire stream system being surveyed. Because foot surveys are not practical or possible in remote rivers in Alaska, alternatives to ground-based field work, such as remote-sensing methods, are necessary to collect salmon habitat data in these areas.

The information needs for assessing change in salmon rearing habitats on federally managed lands in Bristol Bay have not been previously addressed. In 2009, the U.S. Fish and Wildlife Service Togiak National Wildlife Refuge (TNWR), ADFG, and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences collaborated

to address these needs by creating a juvenile salmon abundance and freshwater-habitat monitoring program. The goals of the project were to collect spatially referenced, high-resolution data on fish abundances and freshwater-habitat quality and quantity for long-term monitoring and assessment of habitat change on TNWR lands. Two graduate projects were undertaken to accomplish TNWR's goals; my project identified the types of freshwater habitats that are important for production of juvenile salmon and illustrated the relationships between juvenile Pacific salmon abundance and the physical characteristics of their rearing habitats. A concurrent graduate project used a decision-based fusion approach to analyze multispectral digital imagery and evaluated the accuracy of using remote-sensing methods to classify and quantify important salmon rearing habitats (Woll 2012). The combined results served as estimates of fish abundance and habitat quantity in the Kulukak River for assessment of climate-induced change in the future. This thesis is the presentation and synthesis of my results in the context of global fisheries management and habitat conservation.

In chapter one, I explored patterns of juvenile salmon abundance in relation to the quantity of four categorical in-stream habitat classes (eddy drop zones, pools, riffles, and runs). Habitat quantities were derived from aerial photographs in which the unique properties of each habitat type were used to classify each pixel using a computer-based GIS program (see Woll 2012 for detailed methods). I estimated juvenile salmon abundances in a random sample of habitat units belonging to one of the four in-stream habitat classes. The results from this study objective were estimates of juvenile coho and sockeye salmon abundance per unit area in each categorical in-stream habitat class (i.e., density by in-stream habitat class) and an estimate of the total abundance of juvenile coho and sockeye salmon by in-stream habitat class (i.e., density multiplied by habitat quantity).

In chapter two, I quantified relationships between juvenile coho and sockeye salmon densities and the physical features of their rearing habitats. I used ground-based field methods to measure depth, water velocity, substrate composition, and proportional area of in-stream cover by large wood, undercut banks, and overhanging riparian

vegetation. Analyses of the relationships between species densities and habitat variables revealed that in-stream cover was positively related to coho and sockeye salmon density, while depth and velocity were both negatively related to fish density.

The results of my study indicate that in-stream cover is an important component of freshwater rearing habitat for coho and sockeye salmon. Each species responds differently to the substrate composition of their habitats, which is tied to life-history differences between these two species. As a result, there is a need to monitor and conserve off-channel, backwater habitats that are used by summer-rearing juvenile Pacific salmon. Doing so will foster management of salmon-bearing ecosystems that is responsive to changes in climate and land use and will promote the long-term sustainability of Pacific salmon in Bristol Bay.

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Chapter 1: Estimation of coho and sockeye salmon density and abundance by habitat class[1]

1.1 Abstract

The quantity of freshwater rearing habitat plays a significant role in the dynamics of Pacific salmon *Oncorhynchus* spp. Climate-induced and anthropogenic changes to freshwater landscapes have the potential to alter those dynamics in a way that negatively affects freshwater fisheries. To understand these impacts, monitoring of freshwater habitat quantity and the abundance of freshwater-rearing fish is essential. This study assessed relationships between the abundance of stream-type juvenile coho salmon *O. kisutch* and sockeye salmon *O. nerka* and rearing habitat quantity in the Kulukak River, Alaska. In July 2010, multiple-pass depletion electrofishing was used to enumerate juvenile salmon and aerial image data to quantify total area of habitat by class. The largest proportions of freshwater habitat were comprised of runs (71%) and eddy drop zones (i.e., backwater areas; 44%) in the East Fork and West Fork study areas, respectively. The highest densities of juvenile coho and sockeye salmon were estimated in eddy drop zones (2.22 and 1.32 fish·m^{-2}, respectively) and the lowest densities in riffles (0.22 and 0.05 fish·m^{-2}, respectively). Total abundance estimates of coho and sockeye salmon in the moderate-gradient East Fork study area were highest in runs and eddy drop zones, respectively (45,249 and 22,258, respectively). In the floodplain West Fork study area, total abundances of coho and sockeye salmon were highest in eddy drop zones (22,142 and 97,625 fish, respectively). Coho salmon densities and total abundances were higher than sockeye salmon, regardless of habitat class. This study showed that coho and sockeye salmon differ in habitat use during summer rearing periods, highlighting the need to assess the unique habitat relationships of stream-rearing fishes to understand the potential consequences of climate and anthropogenic change.

[1]Coleman, J. M., and T. M. Sutton. 2013. Juvenile coho and sockeye salmon density by habitat class in the Kulukak River, Alaska. Prepared for submission in Transactions of the American Fisheries Society.

1.2 Introduction

Freshwater fish habitat is changing on a global basis as a consequence of shifting climatic regimes and growing anthropogenic influences. The effects of these changes on Pacific salmon *Oncorhynchus* spp. and their habitats ultimately depend on the life-history characteristics associated with particular stocks (Hilborn et al. 2003). Because salmon stocks are highly adapted to their natal rivers, predicting these effects on a regional level is particularly challenging. However, more important in ensuring the sustainability of Pacific salmon stocks is the maintenance of the diversity of those adaptations and subsequent functioning of the ecosystems salmon inhabit (Beechie et al. 2006). Identification and mitigation of climate-induced and anthropogenic changes to freshwater ecosystem function requires cataloging and long-term monitoring of salmon and their critical habitats.

The most pervasive environmental influence on salmon in subarctic coastal ecosystems is the climate. Climate predictions for subarctic riverine habitats include temperature increases and changes in precipitation and hydrologic regimes (Poff et al. 1997; Meehl et al. 2007). Warmer air temperatures at northern latitudes will result in more precipitation falling as rain during winter and reduced summer precipitation (Wigley 1999; Meehl et al. 2007). Temperature increases may also lead to a lowering of summer groundwater tables and drying of coastal wetlands via increased evaporation and plant evapotranspiration (Rouse et al. 1997; Poff et al. 2002; Walsh et al. 2005). Furthermore, warmer air temperatures are linked with warmer freshwater temperatures because shallow, turbulent streams readily mix heat and oxygen from the surrounding atmosphere (Eaton and Scheller 1996; Scavia et al. 2002). Changes in precipitation patterns are projected to lead to changes in the hydrologic regimes of many rivers and streams, including increased magnitude and frequency of winter flood events, decreased ice cover and high-elevation snowpack, earlier but diminished spring flood events, and decreased summer flood events (Scavia et al. 2002; Meehl et al. 2007).

Confounding the negative effects of climate on stream habitats are changes to the surrounding landscapes such as urbanization, agriculture, logging, mining, and

hydropower development (Murphy and Hall 1981; Murphy et al. 1986; Scheurer et al. 2009). Examples of salmon population declines due to these anthropogenic changes are prevalent in the Pacific Northwest; meanwhile, destructive practices continue throughout the range of Pacific salmon (Nehlsen et al. 1991; Baker et al. 1996). In particular, mining and hydroelectric dams proposed for subarctic Alaska have the potential to degrade freshwater habitat via physical damage and destruction that result from road and infrastructure building (ADNR 2005; Woody and O'Neal 2010). Mine operation also involves drawing from and disconnecting subsurface and surface hydrology, further reducing the amount of in-stream habitat (Woody and O'Neal 2010). Hydroelectric dams disrupt the natural flow regime and have been shown to alternately flood and fragment habitats in response to daily and hourly electricity demands (Geist et al. 2008; Young et al. 2011). In addition, dam and reservoir walls and road culverts create barriers to fish passage, thereby increasing the effort needed for fish to migrate upstream as spawning adults and downstream as smolts (Bingham and Harthorn 2000). As human populations continue to grow in Alaska and throughout the developing world, so too will the need for alteration of their landscapes. Left unchecked, these changes drastically reduce the quantity of critical salmon habitats.

The quantity of available in-stream habitat plays a crucial role in the freshwater rearing stage of salmon development and is sensitive to changing environmental conditions (Mason 1976; Kocik and Ferreri 1998). Reductions in habitat quantity, caused by above-average temperatures and extended summer low-flow periods, and water withdrawal from mining and hydropower operations, can have negative impacts on individual- and population-level dynamics of juvenile Pacific salmon (Quinn and Peterson 1996). Specifically, drying of in-stream habitats can lead to overcrowding, including increased intraspecific competition and decreased individual growth. Sufficient freshwater growth is needed to maximize individual survival during smolt outmigration (Quinn 2005). Habitat fragmentation, in which juveniles are cut off from drifting food resources and oxygenated water, may also result from drought-induced reductions in habitat quantity. Conversely, excessive flows from hydroelectric dam releases can flush

juvenile fish out of rearing habitats and greatly increase mortality. Bauersfeld (1978) reported a total loss of 59% of a Columbia River, Washington, salmon fry population as a result of hydropower-related fluctuations in habitat quantity. The sensitivity of freshwater rearing salmon to the stream environment highlights the need to understand the relationships between habitat quantity, fish abundance, and climatic and anthropogenic changes.

Measurements of freshwater habitat quantity and salmon abundance must be taken now to document changes in freshwater ecosystems (Meyer et al. 1999). Baseline abundance and habitat quantity estimates are important for comparison with estimates under future climate and land-use scenarios and for adaptive, effective management of freshwater ecosystems. In addition, characterizing the extent of seasonal, interannual, and spatial variability of fish abundance and habitat quantity is necessary for managers to be able to recognize when habitat quantity or fish abundance are outside this range (Rosenfeld and Hatfield 2006). For example, it is possible for land managers to propose mitigatory or remedial actions, such as conservation, establishment of wilderness areas, or habitat restoration when the quantity of habitat exceeds a minimum threshold. While restoration is not yet a major concern in Alaska, these actions are ubiquitous throughout the history of salmon management in western North America. The lessons learned from this history support the need for a comprehensive examination of climatic and anthropogenic changes to salmon habitat.

An extensive body of literature exists on the effects of climate change on freshwater rearing habitat and juvenile Pacific salmon in the Pacific Northwest; however, relatively little work has been done regarding these species in Alaska (e.g., Mote et al. 2003; Beechie et al. 2006; Battin et al. 2007). Further, studies that have been conducted in Alaska have concentrated on the effects of environmental conditions on one or two dominant salmon species in a finite geographical area (e.g., Schindler et al. 2005; Drake and Naiman 2007; Bryant 2009). Given the high degree of climate variability across the large geographic extent of Alaska, coupled with the specialized adaptations of salmon to their natal rivers, findings from such studies are seldom universal (Carle and Strub 1978;

Taylor 1991). It is therefore critical to expand our knowledge of the influences of climate on Pacific salmon to include areas of Alaska that have not previously been studied.

Myriad stream-assessment studies have used a variety of methods to count juvenile salmon on a watershed scale with varying levels of bias and precision (e.g., Mahon 1980; Hankin 1984; Hagen and Baxter 2005; Rosenberger and Dunham 2005). Ground-based techniques are extremely time intensive and, as a result, a relatively small number of samples are collected (Williams et al. 2004). This contributes to decreased precision in estimates of salmon abundance and habitat quantity. In addition, constructing an *a priori* sampling frame of in-stream habitats is often impossible, and in many cases researchers must choose sampling units subjectively (i.e., units that are accessible or convenient to sample; Platts et al. 1983; Dolloff et al. 1993). The resulting bias is difficult to characterize, especially in studies where sample sizes are small (Hankin and Reeves 1988). Without validation by known abundance or habitat quantity values that require prohibitively expensive, destructive, or time-consuming methods (e.g., rotenone, dual-gear sampling), such estimates are reported as absolute values without estimates of associated variability, including bias and precision (Rosenfeld 2003; Rosenberger and Dunham 2005). This study is one of few to link known values of habitat quantity derived from aerial imagery with ground-based fish density data for the purpose of estimating fish abundance. Because this method of estimation is unprecedented, identifying likely sources of bias and poor precision is necessary for making inferences based on the resulting estimates of fish abundance and habitat quantity.

This study was conducted to begin cataloging and monitoring the abundances of juvenile Pacific salmon and the quantity of their freshwater rearing habitats in Bristol Bay, Alaska. Much of the coastal freshwater habitat in Bristol Bay remains unaltered by human development, and is therefore an ideal location for assessment of baseline habitat conditions and for monitoring habitat change. The specific study objectives were to (1) estimate the habitat class-specific densities of freshwater rearing coho *O. kisutch* and sockeye *O. nerka* salmon, and (2) multiply those densities by the measured quantity of

each class to estimate the total abundance of juvenile salmon present in two study areas of a Bristol Bay watershed, the Kulukak River.

1.3 Methods

1.3.1 Study location and study area descriptions

The Kulukak River watershed encompasses 532 km^2 and is located 74 km west of Dillingham, Alaska (Figure 1.1). The river is fed by runoff and snowmelt from the Wood River Mountains as well as groundwater discharge via coldwater springs. It flows south for 73 river kilometers (rkm) before draining into Kulukak Bay of Bristol Bay. Five species of Pacific salmon, anadromous Dolly Varden *Salvelinus malma* and rainbow smelt *Osmerus mordax*, and resident Arctic char *S. alpinus* and round whitefish *Prosopium cylandraceum* have been documented in the drainage (MacDonald 1996; Johnson and Klein 2009; M. Lisac, USFWS, personal communication). The upper river is sinuous and high gradient, with a high degree of valley confinement by steep banks. The middle and lower sections of the river are moderate to low gradient, with high- and low-gradient tributaries flowing in from the east and west, respectively. Riparian vegetation includes wetland sedges *Carex* spp., bluejoint grass *Canadensis calmagrostis*, alder *Almus* spp., and stands of cottonwood *Populus* spp. (Wibbenmeyer 1982).

Two tributary study areas within the Kulukak River drainage were selected for sampling (Figure 1.1). We sampled a subset of the drainage to comply with project budget and time constraints. The East and West Fork study areas were selected because they are documented rearing locations for coho salmon and sockeye salmon (Johnson and Klein 2009). Further, these areas are located in the lower and upper sections of the drainage, respectively, and characterize different geomorphic and hydrologic features (e.g., substrata, slope, valley confinement). The East Fork study area is a third-order stream that contains habitat characteristic of B-type reaches according to the Rosgen (1994) reach-type classification scheme. These reaches have more riffles than pools and a stable profile and banks. Habitat measurements were collected in June 2009 for habitat

units in B-type reaches using methods similar to those described in the methods section of this study. The third-order West Fork study area contained C-type reaches of low gradient, meandering riffle-pool complexes located in the alluvial floodplain of the river. Habitat unit dimensions were measured using a reel tape at ¼, ½, and ¾ perpendicular transects along the unit thalweg. Gradient values were derived from a 3-m spatial resolution digital elevation model. Temperature, salinity, and conductivity were measured at one location in each sampled reach using a handheld YSI model-30 multifunction meter (YSI, Inc., Yellow Springs, Ohio), and the predominant and subdominant substrata were visually estimated in each unit. The mean width, gradient, temperature, conductivity and salinity, and predominant substrata for the two study areas are provided in Table 1.1.

1.3.2 Sampling design

Units within the two study areas were sampled using a stratified two-stage cluster design. The study areas were divided into 100-m reaches, which approximated the recommended reach length necessary to represent a diversity of habitat classes in small streams (Flosi and Reynolds 1994). In the two-stage cluster sample, the study areas were divided into larger, first-stage clusters (i.e., reaches) that were randomly sampled, and smaller second-stage clusters (i.e., habitat units) within each reach that were also randomly sampled. To create a sampling frame of 100-m reaches, shapefiles of each study area were derived from 2.5-m resolution multispectral aerial images that were digitized and georeferenced as part of the National Wetland Inventory (NWI). An unsupervised classification was used to classify pixels from the NWI aerial imagery into water and non-water classes in each study area. Using this classified imagery, wetted edges were delineated and stream centerlines were approximated between banks. The thalweg and banks lines were then divided into 100-m segments and converted to individual polygons and numbered from down- to upstream. Numbered reaches within study areas were randomly selected using R statistical computing software (R Development Core Team 2009). To select second-stage samples, a numbered list of the units by habitat class was created during an initial foot survey of the reach using a modified Bisson et al. (1982) habitat classification scheme (Table 1.2). Units were

assigned to one of four general categories: pools, riffles, glides, and eddy drop zones (EDZ). One unit of each habitat class was randomly selected and surveyed per reach and, when time allowed, additional units were sampled randomly from within the reach (Figure 1.2).

1.3.3 Field methods

1.3.3.1 Electrofishing surveys

Fish and habitat sampling took place from 7 to 27 July 2010, and daily sampling during this period occurred between 0900 and 2100 hours (Alaska Daylight Savings Time). Fish surveys were conducted using multiple-pass depletion electrofishing (Alaska Department of Fish and Game permit #SF2009-062; IACUC protocol #09-43; henceforth referred to as electrofishing). Fish were captured using a battery-powered, pulsed-DC backpack electrofishing unit (model LR-24, Smith-Root, Inc., Vancouver, Washington) employing a four-pass depletion method (settings range: voltage = 288–576 V; frequency = 30 Hz; duty cycle = 12.5%). Prior to electrofishing, 3.2-mm or 4.8-mm knotless mesh block nets were placed at the upstream and downstream ends of each unit to uphold the closed population assumption of the multiple-pass removal estimator (White et al. 1982). Block nets were secured to the streambed using sandbags and to the bank using stakes or terrestrial vegetation using parachute cord. Block nets were visually inspected before each electrofishing pass to ensure closure and that the net was free from gaps or tears. Water temperature and conductivity were measured using a handheld YSI model-30 conductivity meter before beginning fish surveys. The YSI meter was calibrated in the lab using a solution of known conductivity corrected for ambient temperature. Prior to the first electrofishing pass in each unit, the "Quick Setup" option on the electrofisher was selected to automatically adjust the electrofisher settings to match the ambient water conductivity.

Each electrofishing pass started at the downstream block net with the anode ring positioned near the middle of the water column and the rattail cathode trailing behind the electrofisher. Electrofishing proceeded upstream in a zig-zag pattern to the upper block

net, while making sure to thoroughly fish undercut banks and large wood. Fish were netted and placed in a black plastic 18.9-L bucket filled with stream water. After each electrofishing pass, the amount of time elapsed from the electrofisher counter was recorded and reset. Captured fish were anesthetized for five minutes using tricaine methanesulfonate (MS-222) in solution at a concentration of 50 $mg \cdot l^{-1}$ (Eisler and Backiel 1960). Fish were identified to species, counted, and placed in a recovery bucket, and all salmon were measured for fork length to the nearest 1 mm (see Appendix A1 for length-frequency data). When fish resumed swimming activity, they were released downstream of the lower block net. An attempt was made to allow the reach turbidity to settle between passes, although units with very fine sediments took longer to settle than the time needed to measure fish from the previous pass. In these instances, approximately twenty minutes elapsed between passes.

Each electrofishing pass was conducted in the same manner, over the same time duration, and with the same electrofishing unit settings to maintain the assumption of static and equal capture probabilities to the extent possible. To minimize errors in abundance estimates, field personnel were briefed on proper data recording and communication procedures (e.g., filling in data forms completely, rechecking data forms, repeating measurements that were communicated verbally) and trained prior to fish sampling to correctly identify juvenile Pacific salmon species. The crew for each electrofishing pass consisted of one electrofishing unit operator, two netters, and a bucket holder.

1.3.3.2 Habitat inventories

To avoid displacing fish out of the study reach for abundance and density estimates, habitat inventories were completed after fish surveys. Units were assigned to one of four general categories: pools, EDZs, runs, and riffles (Table 1.2; Bisson et al. 1982; Marcus 2002; Marcus et al. 2003). Pools were areas in the main channel with concave streambed morphology, where upward-moving currents were visible on the water surface. Eddy drop zones were attached peripherally to the main channel and were characterized by slow or stagnant water and fine sediments. Runs were relatively long

and deep units with fast-moving water, little or no surface turbulence, and a well-defined thalweg. Riffles were wide, shallow sections with fast-moving water breaking over coarse substrata. Habitat classification in this manner can be subjective; however, using a coarse and qualitative classification scheme was suitable for the objectives of this project and those of Woll (2012), whose aerial imagery data were used to estimate juvenile salmon total abundances (see reference for detailed image processing methods).

Within each unit, physical habitat data were collected (Table 1.3). Thalweg length was measured in segments for each unit with a tape measure and was visually estimated where it could not be directly measured. Wetted width (m) of the unit was measured at the upstream and downstream boundaries and at ¼, ½, and ¾ transects perpendicular to the unit thalweg with a tape measure (Figure 1.3B). Large woody debris was defined as individual pieces greater than 10 cm in diameter and 1 m in length and as aggregates in which at least one piece qualified as LWD (Hauer et al. 1999). Length and width of LWD clusters was measured to the nearest 0.1 m. Three measurements of depth (to the nearest 1 cm) along three transects perpendicular to the thalweg (nine measurements total arranged in a grid pattern) were recorded for each unit. Nine 10-s fixed-point average water velocity (to the nearest 0.01 $m \cdot s^{-1}$) measurements at 60% below the water surface were recorded for each unit using a Flo-Mate^{TM} 2000 electromagnetic velocity meter (Marsh-McBirney, Inc., Frederick, Maryland) mounted on a top-setting wading rod. The velocity meter probe was cleaned and calibrated prior to field work according to the manufacturer's instructions. The Wolman (1954) substrate sampling method was used to measure substrate composition of the unit (Table 1.4). Pebble counts were conducted by walking in a zig-zag pattern from down- to upstream in each unit and picking up one substrate particle every other step. The substrate classification of each particle was estimated visually and called out to and tallied by the data recorder.

1.3.4 Data analyses

Estimates of juvenile salmon density were calculated by computing maximum-likelihood estimates of unit abundances under the assumptions of the generalized removal model, and those estimates were divided by the measured surface area of the unit. For

clarity, the number of fish in an individual unit will be referred to as its abundance, whereas the estimated number of fish in each study area will be referred to as its total abundance. Abundance, density, and total abundance estimates were stratified by species, study area, and by habitat class (EDZ, pool, riffle or run), for a total of 16 strata. The habitat-class strata were grouped by species and study area for clarity: East Fork coho (EFC) and sockeye salmon (EFS) and West Fork coho (WFC) and sockeye salmon (WFS). In several cases, depletions among electrofishing passes did not occur or were not large enough in successive sampling occasions to use the generalized removal model for abundance estimation. Abundance estimates from these units were considered to be in violation of the removal-model assumptions, and were not used to calculate average density values. The failure criterion equation used was that of Otis et al. (1978), where for any value of first capture occasion, k, the criterion was:

$$\sum_{i=k}^{t}(t + k - 2i)u_i \leq 0 \quad , \qquad (1.1)$$

where there were $i = 1, \ldots, t$ sampling occasions and u_j was the number of fish captured on the jth occasion.

1.3.4.1 Model specification: generalized removal model

Maximum-likelihood estimates of abundance in each unit were made using a closed-population generalized removal model (Equation 1.2, denoted M_R; Otis et al. 1978). The M_R model is a generalization of the capture-recapture M_{bh} model in which catches are removed from the population after each sampling occasion. The model assumes behavioral response and individual heterogeneity effects on capture probabilities. Removing fish after capture is equivalent to each fish having a recapture probability of zero on subsequent occasions. The M_R model also assumes that the population is closed over the study (i.e., no births, deaths, immigration, or emigration) and that effort (i.e., length of electrofishing time) is held constant between electrofishing passes. However, because capture probability could vary between sampling occasions, different levels of effort, or both factors additively or interactively, the models $M_{R(pass)}$,

$M_{R(effort)}$, $M_{R(pass+effort)}$, and $M_{R(pass*effort)}$ were used to demonstrate these effects, respectively.

The maximum-likelihood abundance estimator in this study used a notation similar to that of Norris and Pollock (1996), where $_i$ denoted electrofishing pass (i = 1, … , t; t = 3 or 4), and X_i denoted the number of fish caught on the ith pass (e.g., X_1 was the number of fish caught on the first pass, X_4 was the number caught on the fourth pass). The sum of the X_i over all passes, denoted S, was the total number of fish that were captured during the study. The number of fish that were not observed was denoted by X_0. The abundance (estimated number of fish; denoted $\hat{N}$) and the capture probabilities on each sampling occasion in a unit were modeled as a function of X_i and S:

$$P[\{X_1,\ldots,X_t\}]=\frac{N!}{\prod_{i=1}^{t}X_i!(N-S)!}p^{S}(1-p)^{tN-\sum_{i=1}^{t}(t-i+1)X_i} \quad . \qquad (1.2)$$

1.3.4.2 Parameter estimation

Parameter estimates were generated under candidate models M_R, $M_{R(effort)}$, $M_{R(pass)}$, $M_{R(pass+effort)}$, and $M_{R(pass*effort)}$. However, when capture probabilities are different for all passes (as was the case for the latter three candidate models), estimation of abundance is not possible. In such cases, the likelihood is maximized with the final capture probability equal to one, and abundance was spuriously estimated as the number of unique individuals observed in the study (Otis et al. 1978). To avoid this estimation problem in this study, the constraint was imposed that the fourth and final capture probability was equal to the third capture probability. For models including an effort covariate, the final effort value was also constrained to equal effort on the third occasion. Capture histories for individual units were pooled in the design matrix of Program MARK by species and study area (i.e., East Fork coho and sockeye salmon, West Fork coho and sockeye salmon). Theoretically, this allowed for more precise estimation of habitat unit abundance and capture probability (Lukacs 2011). Numerical estimation of abundance, all capture probabilities, and their variances for the candidate models was conducted in R statistical computing software using package “RMark”, which calls the

estimation routines of Program MARK (White and Burnham 1999; R Development Core Team 2009).

1.3.4.3 Goodness-of-fit testing

Currently, there are no generally accepted methods for assessing goodness-of-fit in the structure of closed-population removal models (Otis et al. 1978; Burnham and Anderson 2010). It is recommended in the model inference literature that overdispersion be investigated by manually inflating the overdispersion parameter $\hat{c}$ until the quasi-likelihood adjusted Akaike Information Criterion correction for small sample sizes ($QAIC_c$) of the candidate model set no longer decreases (i.e., until the best possible model fit is achieved). However, using this method on the capture data did not result in any values that achieved the best fit among all candidate models. Choosing a value of $\hat{c}$ that "seems" to create the best fit of the candidate models to the data is not advisable and is often subjective (Burnham and Anderson 2010). To avoid such subjectivity, this method was not used and Akaike's information criterion adjusted for small sample sizes (AIC_c) were used in lieu of $QAIC_c$ values to produce model-averaged parameter estimates.

1.3.4.4 Model selection criteria and model averaging

An information-theoretic approach was used for model selection and model averaging of parameter estimates. Akaike's Information Criterion adjusted for small sample sizes (fewer than 60) was used to identify a plausible set of candidate models (Hurvich and Tsai 1989). This was accomplished by considering models whose delta AIC_c (Δ_m) values were less than the recommended value of two to be included in the plausible model set (Burnham and Anderson 2010). Delta AIC_c values are simply the difference in AIC_c values between the mth model and the AIC_c-selected "best" model. Once this set of R models was defined, parameter estimates under each plausible model were averaged according to their Akaike weights (w_i). The model-averaged parameter estimates are generally derived using Equation 1.3:

$$\hat{\bar{\theta}}_j = \sum_{i=1}^{r} w_i \hat{\theta}_{j,i} \quad , \qquad (1.3)$$

where $\hat{\bar{\theta}}_j$ denoted a model-averaged estimate of θ_j and r represented the subset of models that contained variable j.

1.3.4.5 Unconditional variance estimation

To account for bias resulting from differences in the parameter estimates under the plausible models and those under the unknown, true model (i.e., to incorporate model uncertainty) in the variance estimates of model-averaged parameters, unconditional variance estimates (i.e., those that included model uncertainty) were obtained using the model weights (w_i):

$$\widehat{var}\left(\hat{\bar{\theta}}_j\right) = \left[\sum_{i=1}^{R} w_i \sqrt{\widehat{var}\left(\hat{\theta}_{j,i} \middle| g_i\right) + \left(\hat{\theta}_{j,i} - \hat{\bar{\theta}}_j\right)^2}\right]^2 \quad , \qquad (1.4)$$

where $\hat{\bar{\theta}}_j$ was the model-averaged parameter estimate.

When variance estimates are generated under only the AIC_c-selected "best" model, they are accurate in situations where the best model is equal to the true model. However, it is not possible in observational studies for the researcher to know whether or not the selected model is the true model. Therefore, it is preferable to include model uncertainty in the variance estimates of model-averaged parameters (Burnham and Anderson 2010).

1.3.4.6 Habitat unit area and density calculation

Juvenile salmon densities in each unit were calculated by dividing the removal abundance estimates by the area of each unit sampled. The surface area of each unit was calculated by summing the four trapezoidal areas formed by the b unit boundary and transect widths and thalweg length l (Equation 1.5; Figure 1.3C):

$$\hat{a}_i = \sum_{b=1}^{4} \frac{l}{4} \times \left(\frac{w_b + w_{b+1}}{2}\right) \quad . \qquad (1.5)$$

Estimated densities in each unit ($\hat{d}_i$) were calculated by dividing the abundance estimate from the removal model ($\hat{N}$) in each unit by its area ($\hat{a}_i$). These quantities were averaged to compute estimated mean density ($\bar{\hat{d}}$) separately for each species, study area, and habitat class stratum.

1.3.4.7 Total abundances and total habitat areas

To estimate juvenile salmon total abundances ($\hat{T}_k$), mean fish densities in each habitat class were multiplied by the corresponding total habitat area ($\hat{A}_k$) derived from the aerial imagery of Woll (2012). Detailed methods are presented in Woll (2012), but are summarized here for clarity. Digital aerial images of the study areas were taken with cameras mounted in the belly of an airplane modified with two vertical camera ports. Multiple transects were flown parallel to the study areas to ensure adequate overlap in the images. Three types of images were taken (visible, thermal infrared, and near infrared) and later georeferenced in ArcGIS (version 9.1, Environmental Systems Research Institute, Inc., Redlands, California) and mosaiced using ERDAS IMAGINE (ERDAS, Inc., Atlanta, Georgia). By comparing ground-truthed data (i.e., pixels that were assigned a habitat class in the field) to images, it was determined that several different combinations of bands produced the best information on habitat classes. A supervised classification of these band combinations was then used to assign pixels in the images to one of four in-stream habitat (i.e., EDZ, pool, riffle, and run) or landcover (i.e., wood, gravel, grass, ice/snow) classes. An accuracy assessment of the maximum-likelihood classification scheme determined that 82.5 and 67.5% of habitat classes in the West and East Fork study areas, respectively, were classified correctly.

Composite maps of classified images were delineated into habitat units as polygons, and habitat areas were calculated using the field calculator tool in ArcMap. The total area of units that were connected to the main channel plus those unconnected units within 150 m of the main channel were used to calculate total abundances. Both connected and unconnected units were considered because unconnected units often reconnected to the main channel with increased flows (J. Coleman, UAF, personal observation). The habitat areas were calibrated using the accuracy matrix values (user's

and overall accuracies by habitat class; see results of Woll [2012]) to account for misclassification bias (Grassia and Sundberg 1982). Variance of the total abundances in stratum *k* was calculated using the formula of Schaeffer et al. (1996):

$$\widehat{var}\left(\hat{T}_k\right) = \hat{A}_k^{\,2} \times \widehat{var}\left(\hat{\bar{d}}_k\right). \tag{1.6}$$

1.4 Results

1.4.1 Sample sizes and depletion failures

Sixty habitat units were sampled for electrofishing and measurement of physical habitat variables. Fewer habitat units were sampled in the East Fork than in the West Fork study area. East Fork units were frequently too deep or the current was too fast to be sampled safely or effectively. When a habitat unit was encountered that could not be sampled, another habitat unit was selected randomly from within or near the reach. Of the 23 East Fork habitat units sampled, depletion of coho and sockeye salmon failed in four and seven habitat units, respectively. There were seven and 19 depletion failures for coho and sockeye salmon, respectively, in the 37 West Fork habitat units.

1.4.2 Plausible removal model sets

The more parameterized models (i.e., $M_{R[pass+effort]}$, $M_{R[pass*effort]}$) were most often highly weighted among strata, suggesting that catches in most habitat units were affected by the amount of effort or the electrofishing pass (Appendix A1). Simpler models (i.e., M_R) were favored among habitat classes in which catches were relatively large (e.g., eddy drop zones). Simple models, however, were generally not included in the plausible model sets of pools and runs.

1.4.3 Capture probability effects

Overall, there was very little support for the constant capture probability model (Appendix A1). The additive and interactive effects of pass and effort among species, study area, and habitat class strata were well supported. Evidence in the data for the interactive effect of pass and effort suggested that capture probabilities decreased more

for each successive pass at higher levels of effort. Support for the additive model, on the other hand, suggested that effort and pass independently affected capture probabilities. The weight of evidence for models in which capture probability varied as a function of electrofishing pass was greatest in pool habitats for both species and study areas. In general, effort alone had little effect on whether a fish was captured in pools, riffles, and runs and there was minimal evidence for an effort-only effect in EDZs.

1.4.4 Model-averaged capture probability estimates

Capture probabilities in each stratum were averaged across plausible models according to their evidence weights (Table 1.5). Capture probability estimates ranged from 0.160 ($\hat{p}_1$ for sockeye salmon in West Fork riffles) to 0.803 ($\hat{p}_3$ for sockeye salmon in East Fork runs). Model-averaged capture probabilities for all passes were more similar within than among habitat units (e.g., $\hat{p}_1$ in a habitat unit was more similar to $\hat{p}_2$ in the same habitat unit than $\hat{p}_1$ in another habitat unit of the same class). Factors other than electrofishing pass contribute to variability in capture probabilities and abundance estimates within a habitat unit. When considering habitat units within strata, mean capture probabilities by habitat class tended to increase from the first to the third pass (Figure 1.4). In strata where this trend was not observed, capture probabilities remained constant among passes.

1.4.5 Model-averaged abundance estimates

Abundance ($\widehat{N}$) estimates in each stratum were averaged across plausible models according to their model weights. Model-averaged abundance estimates were used to compute density ($\widehat{d}$) by dividing the estimate in each habitat unit by its habitat unit area. The model-averaged abundance estimates were also averaged by habitat class and are reported, with mean densities and standard errors, in Table 1.6.

Several model-averaged abundances were spuriously estimated as the number of unique individuals captured in a habitat unit, or standard errors and estimates were large (i.e., $1 \cdot 10^7$) and were likely poorly estimated. Model-averaged abundance estimates, especially in pools and runs, commonly had standard errors of zero or near zero. These

estimates were likely invalid and were not used to calculate mean habitat class abundances or densities. Abundance estimates of sockeye salmon in East Fork pools could not be model averaged due to a numerical convergence failure by Program MARK. This occurs when values of the model parameters are estimated to be near their boundaries; for example, when a capture probability is estimated to be very close to zero or one. As a result, mean abundances of sockeye salmon in East Fork pools could not be calculated.

Mean abundances ($\hat{\bar{N}}$) were greater in EDZs than in any other habitat class for coho and sockeye salmon in both study areas. The lowest abundances were in riffles, except for sockeye salmon in the West Fork. Abundances of sockeye salmon were similar between West Fork pools and runs, but were much lower than mean sockeye salmon abundances in West Fork EDZs and riffles. East Fork coho salmon pools and EDZs had similar abundances (173 ± 14 and 123 ± 38, respectively), a finding not observed in other strata. Overall, higher coho salmon abundances were found in East Fork EDZs than any other stratum ($\hat{\bar{N}}_{\text{EFC, EDZ}}$ = 173 ± 14; $\hat{\bar{N}}_{\text{EFC, pool}}$ = 123 ± 38, $\hat{\bar{N}}_{\text{EFC, riffle}}$ = 52 ± 14; $\hat{\bar{N}}_{\text{EFC, run}}$ = 95 ± 8). Coefficients of variation for salmon abundances (CV = [SD/mean]·100) were high and ranged from 6% for coho salmon in East Fork pools to 214% for sockeye salmon in East Fork riffles.

1.4.6 Mean density by habitat class

Mean salmon densities ($\hat{\bar{d}}$) varied between study area and species strata (Table 1.6). Eddy drop zones in all strata had the highest densities of juvenile salmon ($\hat{\bar{d}}_{\text{EFC, EDZ}}$ = 2.22 ± 0.30, $\hat{\bar{d}}_{\text{EFS, EDZ}}$ = 1.32 ± 0.18, $\hat{\bar{d}}_{\text{WFC, EDZ}}$ = 2.54 ± 0.25, $\hat{\bar{d}}_{\text{WFS, EDZ}}$ = 0.58 ± 0.08). With the exception of sockeye salmon in the West Fork, fish densities in EDZs were higher than one fish·m^{-2}. Mean coho salmon densities in pools, riffles, and runs, except for East Fork pools, were less than one fish·m^{-2} ($\hat{\bar{d}}_{\text{EFC, pool}}$ = 1.86 ± 0.99). Coho salmon densities among all habitat classes in both study areas were higher than sockeye salmon densities. Both species showed similar patterns in density among habitat classes; EDZs had the highest density, with other habitat classes having markedly lower densities. After

EDZs, densities decreased in varying order among habitat classes. Riffles and runs in both study areas generally had lower densities for both species than pools and EDZs. Coefficients of variation of densities were moderate, and ranged from 37% (sockeye salmon in West Fork runs) to 5% (coho salmon in East Fork runs).

1.4.7 Total habitat area and total abundances

A total of 192,648 m^2 of habitat were digitally photographed and classified in the concurrent study ($\hat{A}_{\text{East Fork}}$ = 105,971 m^2, $\hat{A}_{\text{West Fork}}$ = 86,714 m^2; Table 1.7). Habitat classes with the largest habitat area differed between the two study areas (Figure 1.7). In the East Fork study area, runs comprised 71% of the total habitat area, whereas EDZs comprised 44% of the habitat area in the West Fork (Woll 2012; $\hat{A}_{\text{EFC, run}}$ = 74,907 m^2, $\hat{A}_{\text{WFC, EDZ}}$ = 38,480). Riffles comprised the smallest proportional habitat area in the East (4%) and West (6%) Forks. Pools accounted for only a slightly larger proportion of habitat area than riffles (9 and 18% in the East and West Forks, respectively). The East Fork was characterized by high velocity and deep and wide run habitat, whereas the West Fork contained mostly low velocity EDZ habitat and a relatively large amount of unconnected habitat.

Total abundance estimates of juvenile coho and sockeye salmon varied by habitat class and study area (Figure 1.8). The combined total abundance of both species in both study areas was 268,469 fish (Table 1.8). Total coho salmon abundance among all habitat classes was larger in the West Fork than in the East Fork ($\hat{T}_{\text{WFC}}$ 121,064, $\hat{T}_{\text{EFC}}$ = 102,134), whereas total sockeye salmon abundances were similar between study areas ($\hat{T}_{\text{EFS}}$ = 22,484, $\hat{T}_{\text{WFS}}$ = 22,790). Of the strata in which abundances and densities were estimated, riffles had the fewest numbers of coho and sockeye salmon in both study areas ($\hat{T}_{\text{EFC, riffle}}$ = 1,393, $\hat{T}_{\text{WFC, riffle}}$ = 1,137, $\hat{T}_{\text{EFS, riffle}}$ = 224, $\hat{T}_{\text{WFS, riffle}}$ = 647). Large proportions of the total abundance were found in EDZ habitats (99, 81, and 97% in East Fork sockeye, West Fork coho, and West Fork sockeye strata, respectively).

The variability of total abundance estimates was generally higher than that of mean density estimates, but lower than that of mean abundance estimates. Coefficients of total abundance variation ranged from 9% for coho salmon in the East Fork study area to

82% in the West Fork. The coefficient of variations of both species' mean density ranged from 5 to 37%, and habitat unit abundance CVs ranged from 6 to 214%. There were no consistent patterns in CVs for total abundances among species, study area, or habitat class.

1.5 Discussion

This study quantified the available rearing habitat and abundances of juvenile coho and sockeye salmon in two study areas of the Kulukak River drainage. The highest densities of juvenile coho and sockeye salmon were found in slow-moving, off-channel eddy drop zone (EDZ) habitats. However, multiple sources of variability (e.g., first- and second-stage sampling variance, model selection uncertainty) lead to poor precision in abundance and density estimates. Bias, both in capture probabilities and abundance estimates, is a common problem in removal sampling methods and although our study did not focus on quantifying bias, some of the factors typically associated with bias in removal-sampling studies were observed. These factors are discussed and recommendations are made for future applications of the methods presented here.

1.5.1 Habitat-unit abundance and density estimates

Abundance and density estimates of juvenile coho and sockeye salmon in both study areas were highest in EDZs. In contrast to the findings of this study, Nickelson et al. (1992) found juvenile coho salmon density to be highest in pools during summer low flow periods in Oregon coastal streams. The authors also reported that densities of juvenile coho salmon were highest in alcoves and backwater pools (i.e., EDZs) during winter and spring, respectively. These dissimilarities could be explained by differing hydrologic regimes between the Kulukak River and Oregon coastal streams. In subarctic Alaska, periods of low and high flow occur during winter and spring, respectively, with flows tapering to base levels in early autumn. Departures from Pacific Northwest patterns in seasonal juvenile coho salmon distribution have also been reported for salmon-bearing streams in the Great Lakes region, where hydrologic regimes are similar to those of

streams in coastal Alaska (Healy and Lonzarich 2000). This study revealed that EDZs are highly used habitats when connected to the main channel, but fish may migrate to mainstem habitats (e.g., pools) as flows decrease and off-channel habitats become disconnected and/or frozen (Brown et al. 2011). In early May 2010, some of the off-channel EDZs that were sampled during July 2010 were frozen solid and likely inaccessible to fish (J. Coleman, UAF, personal observation).

Although the highest densities of coho and sockeye salmon were found in the same habitats, mean sockeye salmon densities were lower than coho salmon densities across all habitat types. We attributed this finding to the rarity of stream-rearing salmon across the species' range (Taylor 1991). Although rare, this life-history form has been observed in the Stikine River, British Columbia, where some sockeye salmon stocks rear in Tahltan Lake. However, others have adapted to side-channel habitats in the lower river, far from nursery lakes (Wood 1995; Johnson and Klein 2009). The origins of stream-type sockeye salmon are not well understood and, as a result, speculation about the causal mechanisms of this life-history type or why stream-rearing sockeye salmon were less abundant than coho salmon is beyond the scope of this study.

Precision of abundance and density estimates was generally poor due to multiple sources of variability. Catches were variable between habitat units, even among those of the same habitat class. The variability in catches lead to abundance estimates that were moderately variable, with coefficients of variation (CVs) ranging from 8 to 30%. Mean density estimates were considerably more variable than abundance estimates, with CVs ranging from 9 to 82%, but were relatively low when compared to other studies. For example, Anderson and Hetrick (2004) reported CVs of juvenile coho salmon densities from 74% in riffle habitats to 163% in glide (habitats similar to runs) habitats. Inherent variability between habitat units in abundance estimates and variability due to extrapolation of abundances and densities from a sample of habitat units to an entire study area likely contributed to the increased variance in density estimates relative to the variance in abundance estimates (Hankin and Reeves 1988).

1.5.2 Total abundance estimates

For coho salmon, total abundances were highest in East Fork runs, while total abundances of West Fork coho salmon and all sockeye salmon were highest in EDZs. The first result was attributed to the large proportion of available habitat (71%) comprised of runs rather than the densities estimated in them. Bryant and Woodsmith (2009) found that densities of juvenile salmon were more similar among reaches than among habitat units, indicating that the differential capacities of habitat classes to support juvenile salmon may not be evident at larger scales. Additionally, if profitable habitats are fully seeded, as may be the case with EDZs in the East Fork, fish may colonize less suitable but more abundant habitats nearby (Giannico and Healey 1999). The second finding that total abundances of West Fork coho salmon and sockeye salmon were highest among EDZs is likely a result of high densities in EDZs and the large proportion of habitat they comprised in the West Fork. This is in contrast to the finding of Anderson and Hetrick (2004) that juvenile coho salmon abundances in three southwestern Alaska rivers were greatest in pool habitats, followed by run and EDZ habitats. Differences in watershed-scale geomorphology and habitat composition may explain why abundances in this study were different than those reported by Anderson and Hetrick (2004; Wissmar et al. 2010).

1.5.3 Limitations and considerations for future research

1.5.3.1 Sources of bias and imprecision

Variability in density estimates may be either inherent or sampling based. Inherent variability encompasses differences in density due to temporal, environmental, demographic, and spatial processes. Sampling variability in stream-assessment studies comes from the methods chosen to measure fish abundance. High levels of variability often equate to bias (under- or overestimation) or imprecision (wide confidence bounds on estimates). Although we did not explicitly quantify bias or precision, we observed in this study several factors related to both inherent and sampling variability that have been associated with bias and imprecision in other studies.

Capture probabilities, or the likelihood that a fish will be captured on an electrofishing pass, may contribute to biased estimates produced by removal experiments. Several factors can affect capture probabilities, including crew experience and efficiency, behavioral responses of fish to electrofishing (Mahon 1980; Peterson and Cederholm 1984; Peterson et al. 2004), fish size (Anderson 1995; Reynolds 1996), and habitat complexity and water velocity (Rodgers et al. 1992; Thompson and Rahel 1996). Contrary to most removal experiments, capture-probability estimates in this study increased or stayed the same for all electrofishing passes. Speas et al. (2004) found that capture probabilities of rainbow trout *Oncorhynchus mykiss* were greater in turbid waters (≥ 480 nephelometric turbidity units [NTU]) than in clear waters (≤ 10 NTU). Although turbidity was not measured, catches in habitat classes with silt bottoms and stagnant water (i.e., EDZs) were generally larger on the second than the first pass, violating one of the assumptions of the generalized-removal model. This was likely because crew members walked through the habitat unit on the first pass and stirred up sediments that decreased the ability of the fish to avoid electrofishing equipment on subsequent passes.

Positive bias in capture-probability estimates is common in multiple-pass depletion sampling. Peterson et al. (2004) found overestimation of capture probabilities to be positively correlated with percent cover by undercut banks and cross-sectional area of a sampling site. In a study comparing fish sampling techniques, rootwad cover explained 60% of the variation in removal-abundance estimates of juvenile coho salmon (Rodgers et al. 1992). Many of the units we electrofished contained deep undercut banks and large aggregates or LWD rootwads which made netting stunned fish difficult; as a result, capture probabilities in those units may have been overestimated. This is especially true for coho salmon, which we observed using cover more frequently than sockeye salmon (J. Coleman, UAF, personal observation).

In addition to cover, aggregation of sockeye salmon very likely caused heterogeneity in capture probabilities among passes. Although sockeye salmon smolts form groups in response to agitation, this behavior is not the same as the schooling behavior commonly displayed by outmigrating juvenile pink *O. gorbuscha* and chum *O.*

keta salmon (Hoar 1954). In this study, sockeye salmon often moved away from the electrofisher anode in aggregations, and, depending on the size and shape of the habitat unit, would escape capture on all passes (J. Coleman, UAF, personal observation). In some habitat units, however, aggregations of 30 to 100 sockeye salmon were herded to the end of the habitat unit, where most of the group was then captured. This herding effect suggests that capture probabilities of sockeye salmon in the results do not describe the probability of capturing an individual fish, but rather the probability of capturing an entire aggregation. The herding effect was not observed for coho salmon, which do not form aggregations, but stay close to structure in their environment, such as large wood or undercut banks (Hoar 1954).

There was a general lack of precision in density and abundance estimates for juvenile salmon in our study. Poor precision in abundance estimates may be attributed to small sample sizes at fish capture and habitat-unit scales and high inherent variability in fish densities among habitat units. To correct for these problems, it is necessary to sample more habitat units within each stratum and to conduct additional electrofishing passes in units with few captures or poor depletions (Peterson et al. 2004). Conducting more passes confirms that few fish are actually present in the habitat unit and eliminates the possibility that low catch rates are due to low capture probabilities. Additional removal methods better suited to specific habitat classes (i.e., minnow trapping in slow-water habitats) may increase captures sufficiently to improve the quality of abundance estimates (Bloom 1976; Bryant 2000). Alternatively, a dual-gear approach could be used in which fish are captured using minnow traps, marked and released, then recaptured using single-pass electrofishing to obtain unbiased mark-recapture abundance estimates (Carrier et al. 2009). Regardless of the capture method used, increasing the precision of juvenile salmon abundance estimates is necessary for applications of these methods.

Another source of bias in estimates of freshwater juvenile salmon abundance comes from only sampling during the summer rearing period. This study, as a first attempt at documenting abundance patterns, was not designed to encompass temporal changes in fish abundance. Ground-based fieldwork should be continued to establish

baseline abundance estimates and incorporate interannual variation. Fish sampling must also be repeated at regular intervals to account for temporal changes in fish abundance. Continued intensive, annual ground-based fish surveys to capture temporal trends in density and abundance are essential to producing quality estimates (Knudsen 1999). Once enough data have been collected to establish a baseline estimate of seasonal abundance and density, surveys can be repeated at less frequent intervals using empirical abundance-area relationships. Although many studies also estimate abundance during a short time period (e.g., summer rearing), using aerial imagery is unique in that once reliable estimates of density are established, imagery can quickly be captured to infer fish abundance during the time period of interest. Therefore, it is useful to fishery managers to have estimates of fish density that include temporal variability.

Incorporating temporal variability in abundance estimates could be accomplished by adjusting fish survey protocols; for example, by sampling fish earlier in the season. This solution would be ideal, but is wrought with logistical problems. In subarctic coastal streams, ice break-up can occur as late as mid-May, which makes sampling in streams difficult and dangerous for field crews. Even when ice free, stream temperatures remain just above freezing until day length becomes sufficient to raise water temperatures to average summer daytime temperatures (7°C; J. Coleman, UAF, unpublished data). At or below this threshold, juvenile salmon minimize activity and remain sedentary in association with cover provided by undercut banks and large wood (Hillman et al. 1992; Heggenes et al. 1993; Brown et al. 2011).

1.5.4 Conclusions

In addition to quantifying juvenile salmon abundance and habitat area, this study also characterized unique life-history and behavioral adaptations of Pacific salmon populations. The co-occurrence of stream-rearing juvenile coho and sockeye salmon in the Kulukak River is a prime example of the life-history diversity that would be threatened by abrupt changes to freshwater habitat. Although freshwater ecosystems are in a constant state of flux, such changes typically occur on time scales large enough for species and communities to adapt (Healey 2009). However, when humans

instantaneously alter the landscape via logging, mining, hydropower, and urbanization, or when climate change occurs faster than the historical average, the adaptive abilities of Pacific salmon are not able to keep up (Nehlsen et al. 1991). Under these circumstances, life-history diversity is greatly reduced, and unique stocks of Pacific salmon become phenotypically homogenized and become more vulnerable to alterations to the stream environment (Slaney et al. 1996; Gustafson et al. 2007). Declines in stock diversity are prevalent throughout western North America; in many cases, diversity loss has exceeded a maximum threshold and has resulted in decreased abundance (Nehlsen et al. 1991; Northcote and Atagi 1997; Neville et al. 2007; Tomlinson et al. 2011). Documenting life-history adaptations and understanding the potential consequences of landscape change on the diversity and abundance of Pacific salmon will help fishery and land managers weigh the costs and benefits of resource development in or near freshwater ecosystems.

This study combined measurements of freshwater rearing habitat with habitat class-specific estimates of juvenile Pacific salmon density. It showed that EDZs are highly utilized, abundant habitats for summer-rearing juvenile coho and sockeye salmon. Habitat quantity and juvenile salmon abundance relationships will become invaluable in recognizing and mitigating the effects of a climate and anthropogenic change on salmon productivity, with particular reference to the salmon fisheries in subarctic coastal Alaska.

Table 1.1. Mean habitat measurements (± SE) of B and C reaches (located near the West and East Fork study areas, respectively) in the Kulukak River collected during a 2009 pilot study.

Measurement (± SE)	Reach type	
	B	C
Width	5.4 ± 1.4 m	6.6 ± 1.1 m
Gradient	0.013%	0.003%
Predominant substrata	medium, large gravel	fines, small gravel
Temperature	9.0 ± 0.41 °C	10.2 ± 0.25 °C
Specific Conductance	44.5 ± 2.80 µs/cm	47.2 ± 0.57 µs/cm

Table 1.2. Classification scheme described by Marcus (2002) and Marcus et al. (2003), adapted from Bisson et al. (1982).

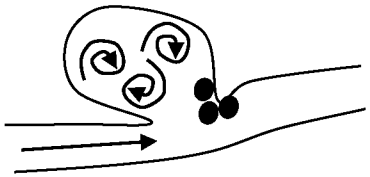
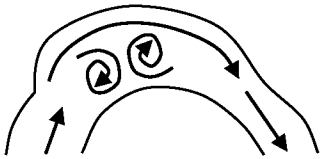
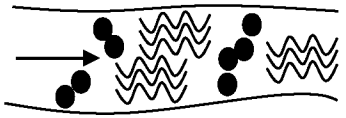
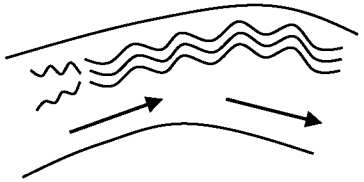
Habitat class	Description	Schematic
Eddy drop zones (EDZ)	Areas of low surface turbulence where backwater circulation deposits fine grained sediments; often peripherally attached to main channel	
Pools	Areas that display little surface disturbance and are usually 0.7 m or more in depth; includes scours located at channel bends	
Riffles	Shallow areas which display significant surface riffles and have slopes of 1-2% in the study area	
Runs	Areas of shallow, smooth flow with coarse gravel substrates or areas that are deeper and slightly more turbulent with a definite thalweg	

Table 1.3. Descriptions of habitat variables measured during habitat inventories.

Habitat variable	Units and description
Class	Categories: pool, riffle, glide, eddy drop zone
Substrate composition	Percent substrata by class
LWD	m^2; mapped onto imagery and length and width measured
Wetted width	m; measured at ¼, ½, and ¾ points perpendicular to thalweg
Thalweg length	m
Depth	m; measured at nine points in each unit
Velocity	$m \cdot s^{-1}$; measured at nine points in each unit
Water temperature	°C; measured at one point in each unit

Table 1.4. Categorical classes used for measuring substrate compositions.

Substrate class	Size class (mm)
Fines	< 2
Small gravel	2–8
Gravel	8–64
Small cobble	64–128
Cobble	128–256
Small boulder	256–512
Boulder	> 512
Bedrock	Solid rock

Table 1.5. Mean (±SE) capture probabilities ($\hat{p}$) of juvenile coho and sockeye salmon captured using four-pass depletion electrofishing in the Kulukak River, July 2010. Capture probabilities were reported for only three passes because the constraint was imposed $\hat{p}_3 = \hat{p}_4$. Dashes (-) represent strata for which estimation of capture probabilities failed.

Stratum	Habitat class	Pass 1	Pass 2	Pass 3
East Fork	EDZ	0.316 ± 0.073	0.312 ± 0.082	0.311 ± 0.091
coho salmon	Pool	0.401 ± 0.065	0.378 ± 0.074	0.471 ± 0.155
	Riffle	0.407 ± 0.147	0.244 ± 0.124	0.338 ± 0.201
	Run	0.389 ± 0.070	0.338 ± 0.089	0.658 ± 0.085
East Fork	EDZ	0.346 ± 0.071	0.508 ± 0.114	0.400 ± 0.148
sockeye salmon	Pool	-	-	-
	Riffle	0.345 ± 0.114	0.303 ± 0.131	0.770 ± 0.194
	Run	0.460 ± 0.176	0.587 ± 0.170	0.803 ± 0.177
West fork	EDZ	0.280 ± 0.100	0.270 ± 0.107	0.259 ± 0.116
coho salmon	Pool	0.408 ± 0.086	0.537 ± 0.094	0.649 ± 0.107
	Riffle	0.374 ± 0.119	0.484 ± 0.139	0.624 ± 0.173
	Run	0.291 ± 0.094	0.492 ± 0.109	0.547 ± 0.133
West Fork	EDZ	0.277 ± 0.138	0.283 ± 0.145	0.292 ± 0.160
sockeye salmon	Pool	-	-	-
	Riffle	0.160 ± 0.264	0.199 ± 0.321	0.253 ± 0.484
	Run	-	-	-

Table 1.6. Mean ± SE abundance, mean ± SE density (fish·m^{-2}), and coefficients of variation (CV) by stratum of juvenile coho and sockeye salmon captured using four-pass depletion electrofishing in the Kulukak River, July 2010. Dashes (-) represent strata for which estimation of abundance and density failed.

Stratum	Habitat class	Mean abundance	Abundance CV	Mean density	Density CV
East Fork	EDZ	173 ± 28	16%	2.22 ± 0.44	52%
coho salmon	Pool	123 ± 5	4%	1.86 ± 0.12	9%
	Riffle	52 ± 8	15%	0.31 ± 0.11	49%
	Run	95 ± 12	13%	0.60 ± 0.03	12%
East Fork	EDZ	171 ± 9	5%	1.32 ± 0.13	25%
sockeye salmon	Pool	-	-	-	-
	Riffle	11 ± 23	214%	0.05 ± 0.01	23%
	Run	-	-	-	-
West Fork	EDZ	154 ± 19	12%	2.54 ± 0.37	36%
coho salmon	Pool	44 ± 24	55%	0.48 ± 0.05	22%
	Riffle	32 ± 7	21%	0.22 ± 0.04	35%
	Run	51 ± 9	18%	0.54 ± 0.20	82%
West Fork	EDZ	49 ± 15	31%	0.58 ± 0.04	10%
sockeye salmon	Pool	-	-	-	-
	Riffle	12 ± 2	20%	0.12	26%
	Run	-	-	-	-

Table 1.7. Total areas (m^2) of habitat units connected to and disconnected from the main channel by study area and habitat class. Areas were calculated by using a decision-based fusion approach to classifying digital aerial images based on the spectral characteristics of each habitat class.

Study Area	Habitat class	Connected	Disconnected	Total	Proportion
East Fork	EDZ	11,318	5,496	16,813	0.16
	Pool	8,117	1,672	9,789	0.09
	Riffle	3,400	1,061	4,461	0.04
	Run	59,177	15,730	74,907	0.71
			Total	105,971	
West Fork	EDZ	24,316	14,164	38,480	0.44
	Pool	14,684	932	15,615	0.18
	Riffle	4,148	1,142	5,290	0.06
	Run	24,170	3,159	27,329	0.32
			Total	86,714	

Table 1.8. Total abundance (± SE) and coefficients of variation (CV) of juvenile coho and sockeye salmon by strata based on four-pass depletion electrofishing estimates of density and estimates of total habitat area. Total habitat areas were calculated by using a decision-based fusion approach to classifying digital aerial images based on the spectral characteristics of each habitat class. Dashes (-) represent strata for which estimation of abundance failed.

Stratum	Habitat class	Total abundance	CV	Stratum total
East Fork	EDZ	37,280 ± 7,363	52%	
coho salmon	Pool	18,212 ± 1,204	9%	
	Riffle	1,393 ± 485	49%	
	Run	45,249 ± 2,416	12%	
				102,134 ± 11,468
East Fork	EDZ	22,258 ± 2,126	25%	
sockeye salmon	Pool	-	-	
	Riffle	224 ± 51	23%	
	Run	-	-	
				22,482 ± 2,177
West Fork	EDZ	97,625 ± 14,220	36%	
coho salmon	Pool	7,533 ± 736	22%	
	Riffle	1,137 ± 232	35%	
	Run	14,770 ± 5,447	82%	
				121,064 ± 20,635
West Fork	EDZ	22,142 ± 1,498	10%	
sockeye salmon	Pool	-	-	
	Riffle	647 ± 120	26%	
	Run	-	-	
				22,790 ± 1,618

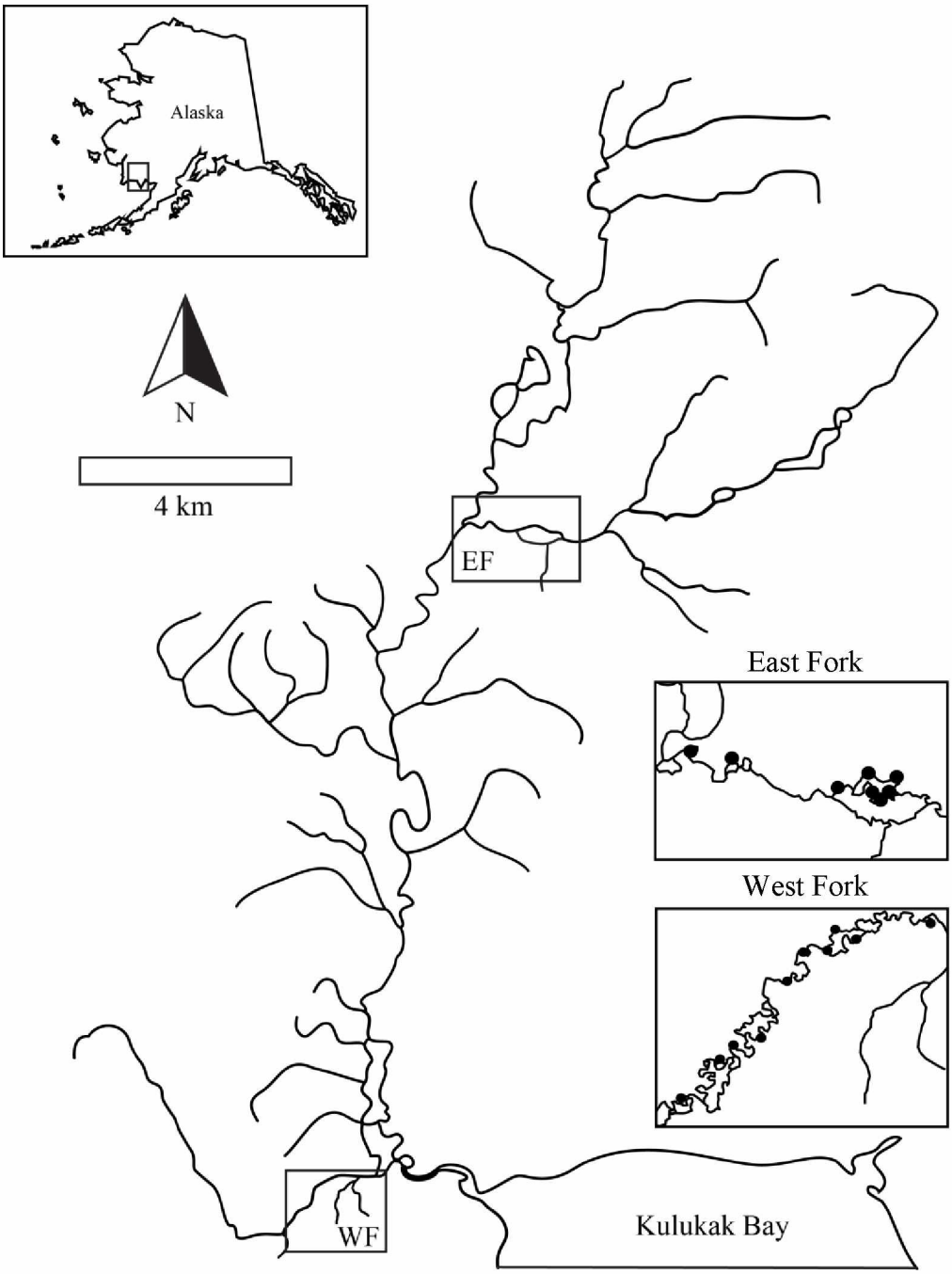


Figure 1.1. Map of the study site, showing the Kulukak River (main map) and its location in Alaska (upper left inset map). The detailed maps of the East and West Fork study areas on the right show the 100-m reaches that were selected (dots) for fish surveys and habitat inventories in each study area. Figure adapted from MacDonald (1996).

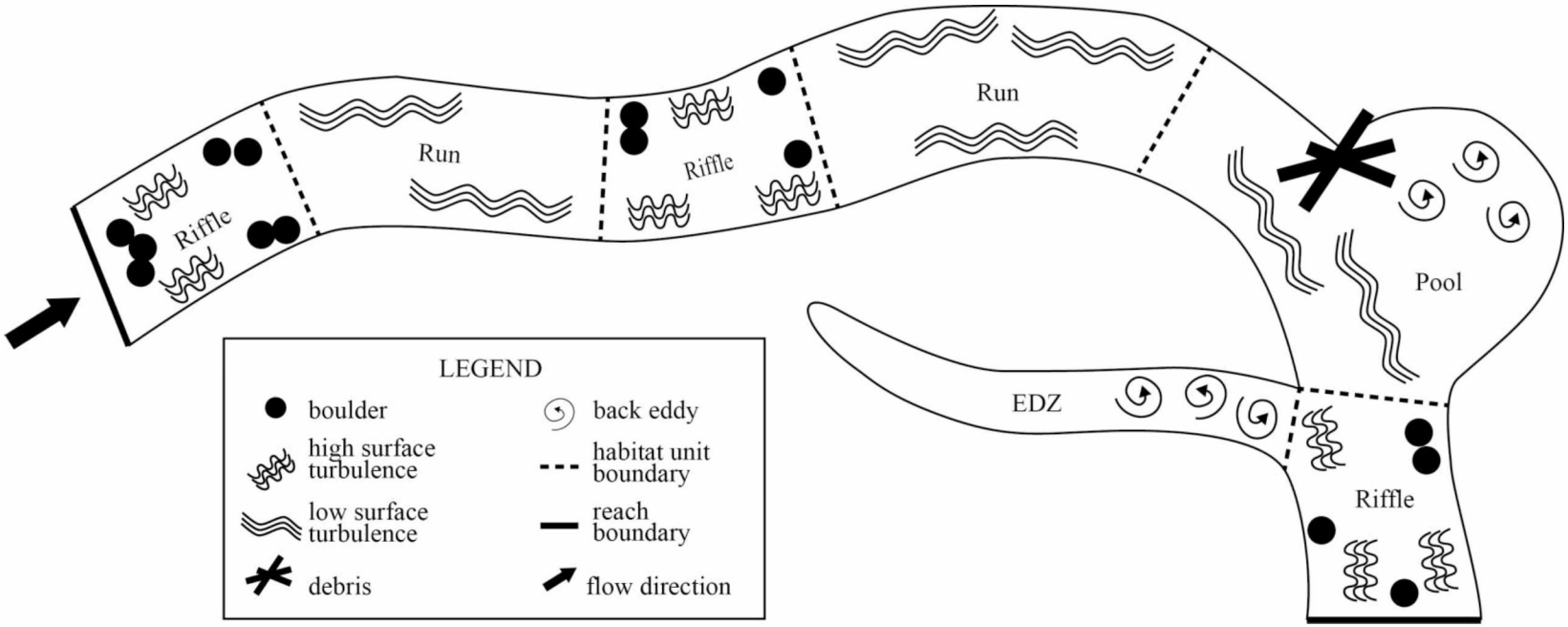


Figure 1.2. Schematic of fish survey and habitat inventory sample reach. In the hypothetical sample reach pictured, the units classified as pool and eddy drop zone (EDZ) habitat would be sampled. Because multiple riffles and runs are located within the sample reach, only one riffle and one run would be randomly selected for habitat measurements and removal electrofishing.

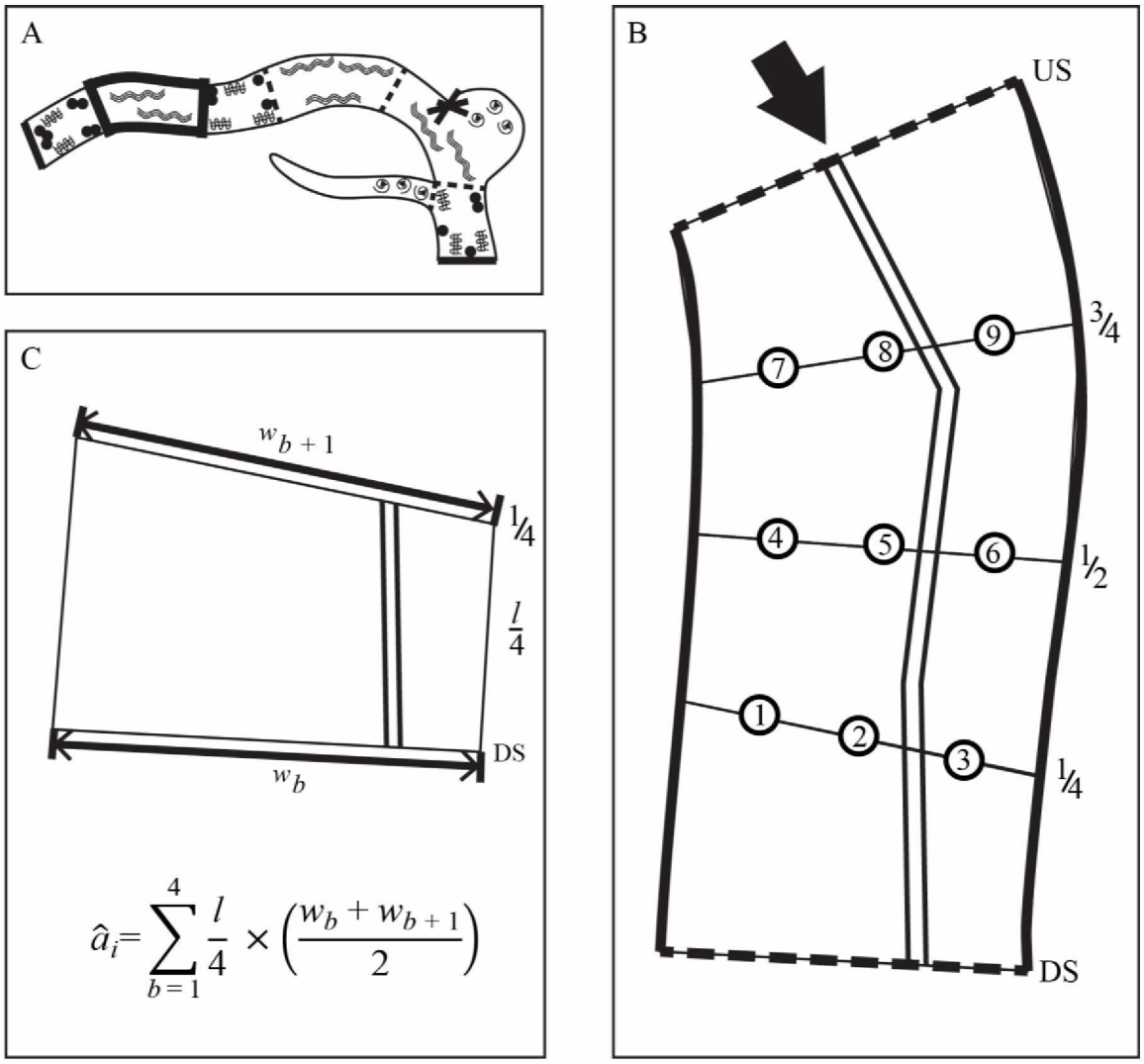


Figure 1.3. Schematic of sample reach (A), habitat unit (B), and habitat unit section and area measurements (C). Panel (A) shows a hypothetical reach with one habitat unit outlined in black. Panel (B) shows the unit thalweg, upstream (US) and downstream (DS) boundaries, and flow direction represented by the double black line, dashed line, and black arrow, respectively. Circled numbers represent locations where depth and velocity measurements were taken on ¼, ½, and ¾ transects. Panel (C) shows width and length measurements and equation used to calculate habitat unit area

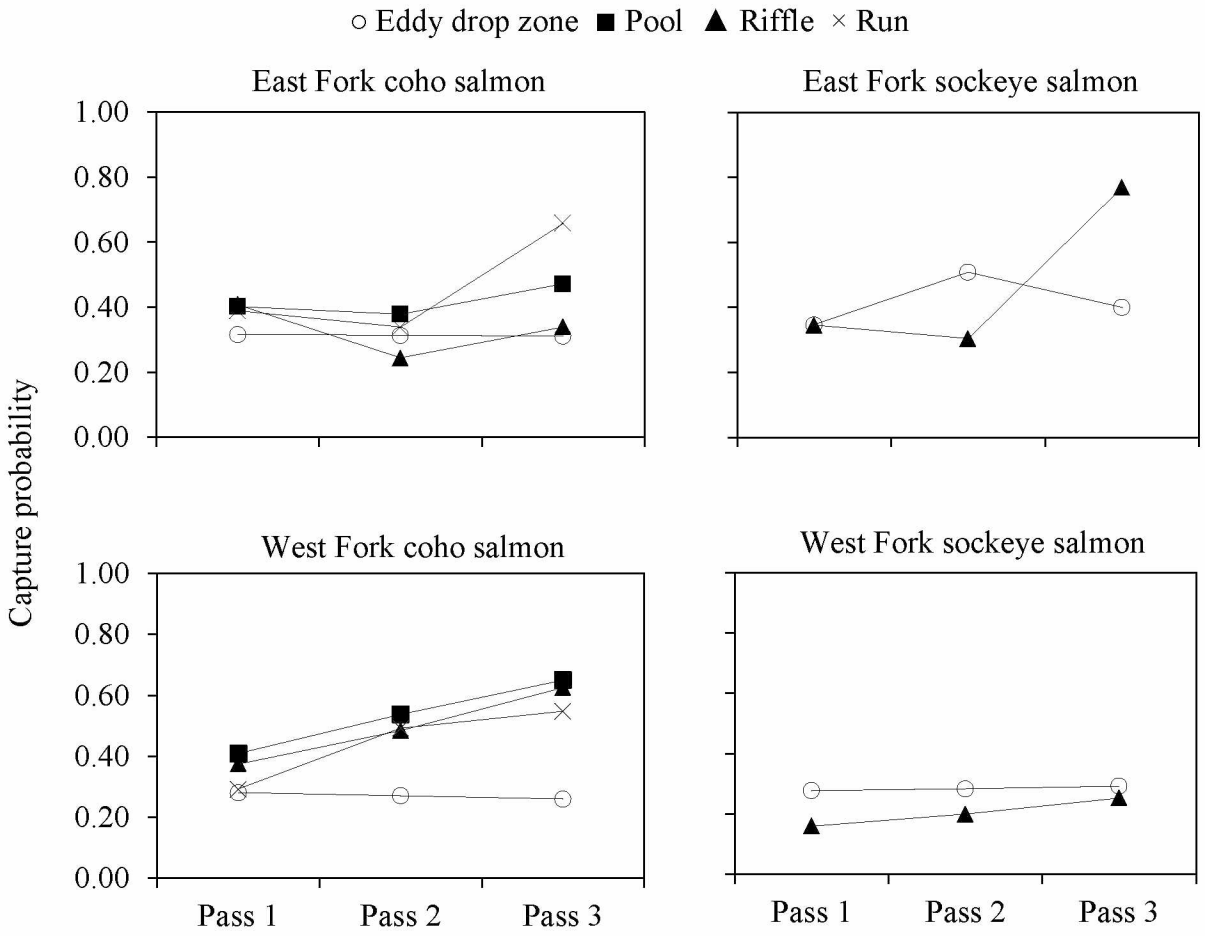


Figure 1.4. Model-averaged capture probabilities ($\hat{p}$) of juvenile coho and sockeye salmon in the East and West Fork study areas (see methods section for details on model averaging). Points represent model-averaged $\hat{p}$ for eddy drop zones (EDZ), pools, riffles, and runs for each of three electrofishing passes ($\hat{p}_3 = \hat{p}_4$). Fish were captured in closed habitat units using four-pass depletion electrofishing in the Kulukak River, July 2010.

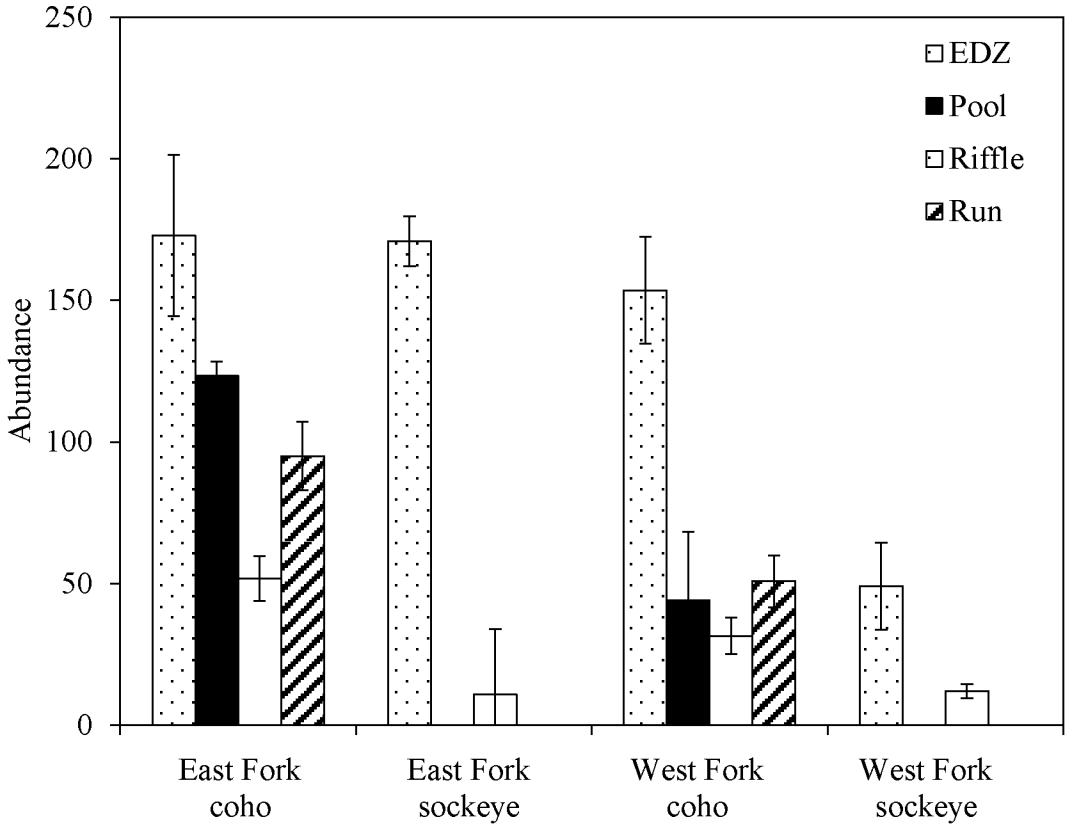


Figure 1.5. Mean (±SE) habitat unit abundances of juvenile coho and sockeye salmon by study area and habitat class. Fish were captured in closed habitat units of four classes (eddy drop zone [EDZ], pool, riffle, and run) using four-pass depletion electrofishing in the Kulukak River, July 2010. Abundance in pools and runs could not be estimated for sockeye salmon in the East and West Fork study areas.

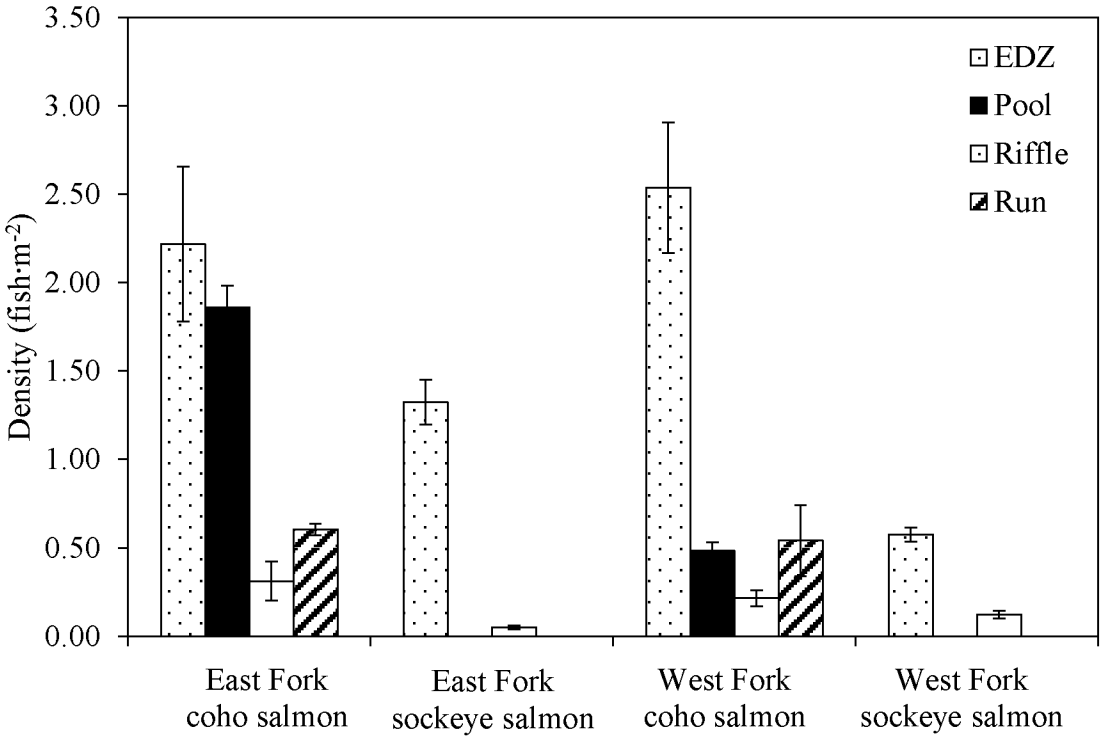


Figure 1.6. Mean (±SE) habitat unit densities (fish·m^{-2}) of juvenile coho and sockeye salmon by study area and habitat class. Fish were captured in closed habitat units of four classes (eddy drop zone [EDZ], pool, riffle, and run) using four-pass depletion electrofishing in the Kulukak River, July 2010. Density in pools and runs could not be estimated for sockeye salmon in the East and West Fork study areas.

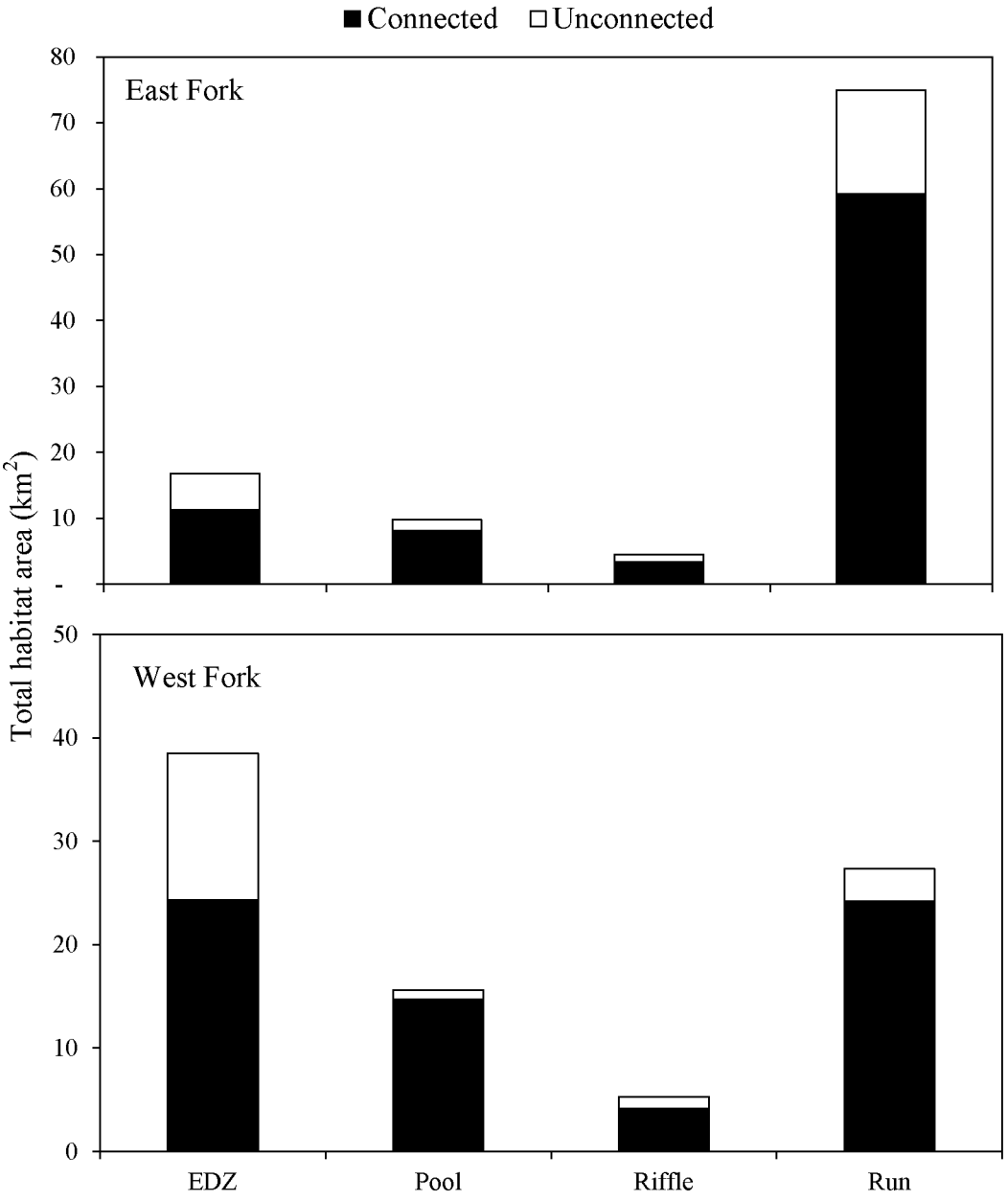


Figure 1.7. Total habitat area (km^2) by class. Areas were calculated by using a decision-based fusion approach to classifying digital aerial images based on the spectral characteristics of each habitat class. Unconnected habitat areas were those that were not connected to the main channel, but were within 150 m of the main channel.

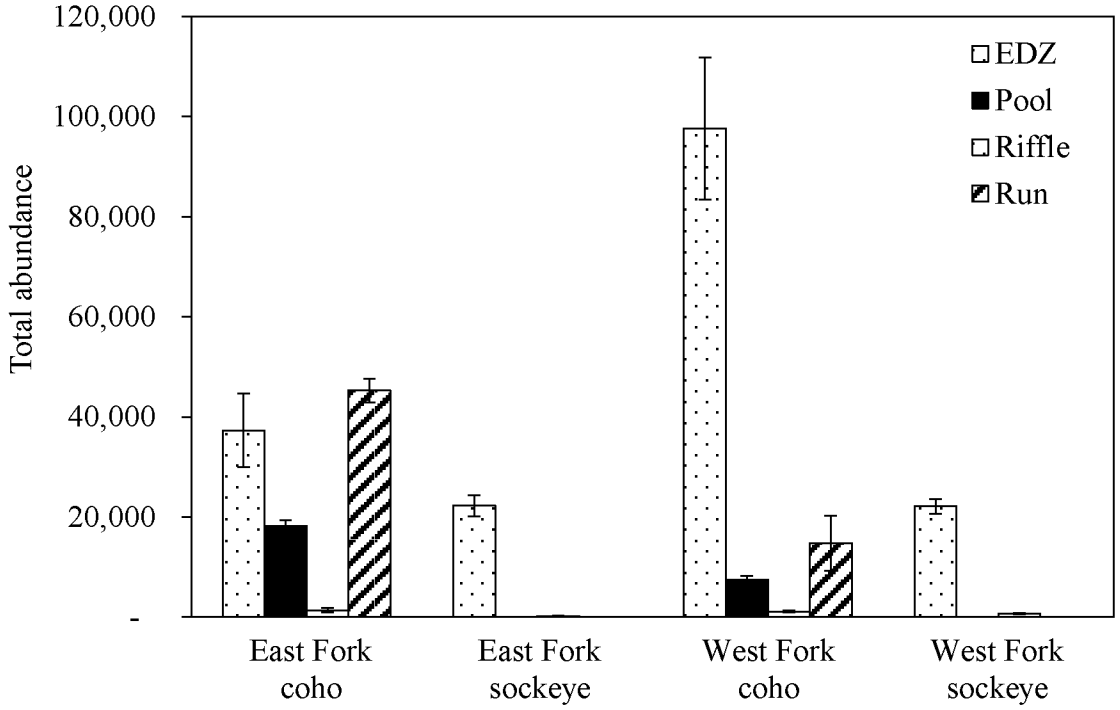


Figure 1.8. Total abundance estimates by stratum with standard errors represented by bars. Total abundance in pools and runs could not be estimated for sockeye salmon in the East and West Fork study areas.

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Chapter 2: Relationships between juvenile coho and sockeye salmon density and physical characteristics of freshwater rearing habitat[1]

2.1 Abstract

Uncertainty in how freshwater habitats may be affected by human- and climate-induced change necessitates collecting baseline data on these habitats and the Pacific salmon *Oncorhynchus* spp. that rear in them. This study quantified relationships between density of stream-rearing juvenile coho salmon *O. kisutch* and sockeye salmon *O. nerka* and proportional area of in-stream habitat features in the Kulukak River, Alaska, in July 2010. In-stream cover by overhanging vegetation and large wood were positively related to density of coho salmon (regression coefficient [RC] = 0.78 and 0.99, respectively) and sockeye salmon (RC = 0.74 and 0.97, respectively). In contrast, depth and velocity were negatively correlated with coho salmon (RC = -1.45 and -2.45, respectively) and sockeye salmon (RC = -0.52 and -1.67, respectively) density. The relationship between density and substrate size, unlike other variables, was positive for coho salmon (RC = 0.08) but negative for sockeye salmon (RC = -0.40). These results suggest that stream-rearing juvenile coho and sockeye salmon are similar in their relationships to physical habitat characteristics, but that key differences exist: 1) coho salmon density was more negatively correlated with depth and velocity than sockeye salmon density, and 2) substrate size was positively and negatively related to coho and sockeye salmon density, respectively. Anthropogenic and climate changes to freshwater habitats are likely to affect juvenile coho and sockeye salmon densities differentially, both in direction and magnitude.

[1]Coleman, J. M., and T. M. Sutton. 2013. Relationships between juvenile coho and sockeye salmon density and physical characteristics of freshwater rearing habitat. Prepared for submission in Transactions of the American Fisheries Society.

2.2 Introduction

The effects of habitat alterations on Pacific salmon *Oncorhynchus* spp. stocks depend on the unique characteristics associated with particular stocks and are complex and difficult to predict (Hilborn et al. 2003). As a result, it is important to maintain the diversity of those characteristics and subsequent functioning of the ecosystems that Pacific salmon inhabit (Beechie et al. 2006). Salmon stocks are diverse in how they relate to the physical environment, particularly in their use of depth, velocity, and physical structure. Quantifying the relationships between salmon and their habitats during critical life stages provides fundamental information for effective land-use and fishery management.

The physical features of freshwater environments offer protection from predators and foraging and growth opportunities for juvenile salmon prior to their migration to the ocean (Nickelson et al. 1992; Quinn and Peterson 1996; Nickelson and Lawson 1998). Previous research on freshwater life stages has identified direct correlations between abundance of juvenile salmon and physical habitat quality, especially the presence of in-stream cover (e.g., Rosenfeld et al. 2000; Anderson and Hetrick 2004; Nemeth et al. 2004). In particular, large woody debris (LWD) and undercut banks (UCB) have been shown to provide refuge from fish predators and energetically taxing water velocities (Butler and Hawthorne 1968; Shirvell 1990; Inoue and Nakano 2001; Crook and Robertson 1999; Suttle et al. 2004). Leaf cover provided by overhanging riparian vegetation offers shade for thermal regulation and visual isolation from avian predators (Murphy and Hall 1981; Welsh et al. 2001). Previous studies have also shown that coho salmon *O. kisutch* establish feeding territories in spaces created by large wood and undercut banks (Dill and Fraser 1984; Burgner 1991). Because growth during freshwater life stages affects survival in subsequent life stages, rearing habitat quality can influence salmon abundance throughout their life cycle (Salo and Bayliff 1958; Chapman 1962; Ebersole et al. 2006).

In addition to in-stream cover, juvenile salmon abundance has also been correlated with water depth, velocity, and substrate size. Water depths and velocities

exceeding favorable ranges have been shown to negatively affect salmon abundance (Bisson et al. 1988; McMahon and Hartman 1989; Beecher et al. 2002). Holding a fixed position in the stream channel while foraging for drifting prey is energetically costly for juvenile salmon; therefore, off-channel areas of slow-moving water are important for conserving energy reserves (Nielsen 1991). Positive relationships between substrate size and juvenile salmonid abundance have also been previously described (e.g., Crouse et al. 1981; Suttle et al. 2004; Bolliet et al. 2005). For example, juvenile coho salmon avoided habitats with fine substrates and silt bottoms with high levels of suspended sediment (> 70 NTU; Bisson and Bilby 1982). Fine substrates may also fill interstitial spaces, which are used by salmon for visual isolation from predators and as velocity refugia (McMahon and Hartman 1989).

An extensive body of literature exists on the relationships between freshwater rearing habitat and juvenile Pacific salmon in the Pacific Northwest; however, relatively little research has been conducted on these same species in Alaska (e.g., Mote et al. 2003; Beechie et al. 2006; Battin et al. 2007). Studies that have been completed in Alaska have concentrated on the effects of environmental conditions on one or two dominant species in a finite geographical area (e.g., Schindler et al. 2005; Drake and Naiman 2007; Bryant 2009). Given the diversity of habitats found throughout the state and the highly specialized adaptations of salmon to their natal systems, findings from specific studies are seldom universal (Taylor 1991). It is critical to expand our knowledge of Pacific salmon and habitat to include areas of Alaska and life histories that have not been studied previously.

The focus of our study is on the ecology of stream-rearing juvenile salmon in Bristol Bay, Alaska. The salmon fisheries in the region have achieved long-term sustainable yield as a result of effective fishery management by a single agency, favorable ocean conditions, and a wealth of phenotypic diversity among its constituent stocks (Hilborn et al. 2003). Catch and escapement data have been recorded for over 150 years, but comparatively little is known about the early life-history stages of Bristol Bay salmon. The abundance of unique freshwater habitats, including deep "fiord lakes"

formed by retreating glaciers during the mid-Pleistocene era, shallow-grade coastal rivers, and off-channel floodplain ponds, has resulted in hundreds of distinct spawning stocks that have each adapted to the fine-scale features of their natal sites (Manley et al. 2001; Gomez-Uchida et al. 2011). Maintaining the diversity of freshwater habitats is essential to protecting the phenotypic diversity of salmon in the Bristol Bay region.

Given ongoing human- and climate-induced changes and the limited knowledge of freshwater dynamics in Alaska, research is needed to understand salmon-habitat relationships. Knowledge of salmon-habitat dynamics will enable land and fishery managers to recognize and mitigate effects of change in order to sustain the function of freshwater ecosystems. The objective of this research was to model the densities of stream-rearing juvenile Pacific salmon as a function of physical habitat variables in discrete habitat units within two tributaries of the Kulukak River in the Bristol Bay drainage, Alaska. The results of our study will explore the relationships between freshwater rearing habitat and juvenile salmon abundance in the Kulukak River, and will contribute to the body of research on salmon-habitat relationships that is essential in understanding how abrupt landscape and climate changes affect Pacific salmon.

2.3 Methods

2.3.1 Study location and study area descriptions

The Kulukak River watershed encompasses 532 km^2 and is located 74 km west of Dillingham, Alaska (Figure 2.1). The river is fed by runoff and snowmelt from the Wood River Mountains as well as groundwater discharge via coldwater springs. It flows south for 73 river kilometers (rkm) before draining into Kulukak Bay of Bristol Bay. Five species of Pacific salmon, anadromous Dolly Varden *Salvelinus malma* and rainbow smelt *Osmerus mordax*, and resident Arctic char *S. alpinus* and round whitefish *Prosopium cylandraceum* have been documented in the drainage (MacDonald 1996; Johnson and Klein 2009; M. Lisac, USFWS, personal communication). The upper river is sinuous and high gradient, with a high degree of valley confinement by steep banks. The

middle and lower sections of the river are moderate to low gradient, with high- and low-gradient tributaries flowing in from the east and west, respectively. Riparian vegetation includes wetland sedges *Carex* spp., bluejoint grass *Canadensis calmagrostis*, alder *Almus* spp., and stands of cottonwood *Populus* spp. (Wibbenmeyer et al. 1982).

Two tributary study areas within the Kulukak River drainage were selected for sampling (Figure 2.1). A subset of the drainage was sampled to comply with project budget and time constraints. The East and West Fork study areas were selected because they are documented rearing locations for coho salmon *O. kisutch* and sockeye salmon *O. nerka* (Johnson and Klein 2009). The East Fork study area is a third-order stream section that contained habitats characteristic of B-type reaches according to the Rosgen (1994) reach-type classification scheme. These reaches had more riffles than pools and a stable profile and banks. Habitat measurements were collected in June 2009 for habitat units in B-type reaches using methods similar to those described in the methods section of this study. The third-order West Fork study area contained C-type reaches of low gradient, meandering riffle-pool complexes located in the alluvial floodplain of the river.

2.3.2 Sampling design

Habitat units within the two study areas were sampled using a stratified two-stage cluster design. The study areas were divided into 100-m reaches, which approximated the recommended reach length necessary to represent a diversity of habitat classes in small streams (Flosi and Reynolds 1994). In the two-stage cluster samples, study areas were divided into larger, first-stage clusters (i.e., reaches) that were randomly sampled, and smaller second-stage clusters (i.e., habitat units) within each reach that were also randomly sampled. We were able to select sample reaches before going in the field, but not habitat units. Shapefiles of each study area derived were from 2.5-m resolution multispectral aerial images that were digitized and georeferenced as part of the National Wetland Inventory (NWI). An unsupervised classification was used to classify pixels from the NWI aerial imagery into water and non-water classes in each study area. Using this classified imagery, wetted edges were delineated and stream centerlines were approximated between banks. The thalweg and banks lines were then divided into 100-m

segments and converted to individual polygons and numbered from down- to upstream. Numbered reaches within study areas were randomly selected using R statistical computing software (R Development Core Team 2009). To select second-stage samples, a numbered list of the units by habitat class was created during an initial foot survey of the reach using a modified Bisson et al. (1982) habitat classification scheme (Figure 2.2). Units were assigned to one of four general categories: pools, riffles, glides, and eddy drop zones. One unit of each habitat class was randomly selected and surveyed per reach and, when time allowed, additional units were sampled randomly from within the reach.

2.3.3 Field methods

2.3.3.1 Habitat variable measurements

Habitat units were assigned one of four general habitat classes: pools, eddy drop zones (EDZ), runs, and riffles (Table 2.1; Bisson et al. 1982; Marcus 2002; Marcus et al. 2003). Pools were considered to be areas in the main channel with concave streambed morphology, where upward-moving currents were visible on the water surface. Eddy drop zones were attached peripherally to the main channel and were characterized by slow or stagnant water and fine sediments. Runs were relatively long and deep units with fast-moving water and little or no surface turbulence, and a well-defined thalweg. Riffles were wide, shallow sections with fast-moving water breaking over coarse substrata. Habitat classification in this manner can be subjective; however, using a coarse and qualitative classification scheme was suitable for the objectives of this project and those of Woll (2012), whose aerial imagery data were used to estimate juvenile salmon population abundances (see reference for detailed image processing methods). Although all habitat units were classified, this information was not used to compare fish-habitat habitat relationships between classes due to small sample sizes.

Within each unit, dimensional measurements and physical habitat data were collected (Table 2.2). Thalweg length was measured in segments for each unit with a tape measure. The thalweg was visually estimated where it could not be directly measured. Wetted width (m) of the unit was measured at the upstream and downstream boundaries,

and ¼, ½, and ¾ transects perpendicular to the unit thalweg with a tape measure. Large woody debris was defined as individual pieces greater than 10 cm in diameter and 1 m in length and as aggregates in which at least one piece qualified as LWD (Hauer et al. 1999). Length and width of LWD clusters was measured to the nearest 0.1 m. Three measurements of depth (to the nearest 1 cm) along three transects perpendicular to the thalweg (nine measurements total arranged in a grid pattern) were recorded for each unit. Nine 10 s fixed-point average water velocity (to the nearest 0.01 m·s-1) measurements at 60% below the water surface were recorded for each unit using a Flo-MateTM 2000 electromagnetic velocity meter (Marsh-McBirney, Inc., Frederick, Maryland) mounted on a top-setting wading rod. The velocity meter probe was cleaned and calibrated prior to field work according to the manufacturer's instructions. The Wolman (1954) substrate sampling method was used to measure substrate composition of the unit (Table 2.3). Pebble counts were conducted by walking in a zig-zag pattern from down- to upstream in each unit and picking up one substrate particle every other step. The substrate classification of each particle was estimated visually and called out to and tallied by the data recorder.

2.3.3.2 Electrofishing surveys

Fish and habitat sampling took place from 7 to 27 July 2010, and daily sampling during this period occurred between 0900 and 2100 hours (Alaska Daylight Savings Time). Fish surveys were conducted using multiple-pass depletion electrofishing (Alaska Department of Fish and Game permit #SF2009-062; IACUC protocol #09-43; henceforth referred to as electrofishing). Fish were captured using a battery powered, pulsed-DC backpack electrofishing unit (model LR-24, Smith-Root, Inc., Vancouver, Washington) employing a four-pass depletion method (settings range: voltage = 288–576; frequency = 30 Hz; duty cycle = 12.5%). Prior to electrofishing, 3.2-mm or 4.8-mm knotless mesh block nets were placed at the upstream and downstream ends of each unit to uphold the closed population assumption of the multiple-pass removal estimator (White et al. 1982). Block nets were secured to the streambed using sandbags and to the bank using stakes or terrestrial vegetation using parachute cord. Block nets were visually inspected before

each electrofishing pass to ensure closure and that the net was free from gaps or tears. Water temperature and conductivity were measured using a handheld YSI model-30 conductivity meter, calibrated in the lab using a solution of known conductivity corrected for ambient temperature (YSI, Inc., Yellow Springs, Ohio) before beginning fish surveys. Prior to the first electrofishing pass in each unit, the "Quick Setup" option on the electrofisher was selected to automatically adjust the electrofisher settings to match the ambient water conductivity.

Each electrofishing pass started at the downstream block net with the anode ring positioned near the middle of the water column and the rattail cathode trailing behind the electrofisher. Electrofishing proceeded upstream in a zig-zag pattern to the upper block net, while making sure to thoroughly fish undercut banks and large wood. Fish were netted and placed in a black plastic 18.9-L bucket. After each electrofishing pass, the amount of time elapsed from the electrofisher counter was recorded and reset. Captured fish were anesthetized for five minutes using tricaine methanesulfonate (MS-222) in solution at a concentration of 50 $mg \cdot l^{-1}$ (Eisler and Backiel 1960). Fish were identified to species, counted, and placed in a recovery bucket, and all salmon were measured for fork length to the nearest 1 mm (see Appendix A1 for length-frequency data). When fish resumed swimming activity, they were released downstream of the lower block net. An attempt was made to allow the reach turbidity to settle between passes, although units with very fine sediments took longer to settle than the time needed to measure fish from the previous pass. In these instances, approximately twenty minutes elapsed between passes.

Each electrofishing pass was conducted in the same manner, over the same time duration, and with the same electrofishing unit settings to maintain the assumption of static and equal capture probabilities to the extent possible. To minimize errors in abundance estimates, field personnel were briefed on proper data recording and communication procedures (e.g., filling in data forms completely, rechecking data forms, repeating measurements that were communicated verbally) and trained prior to fish sampling to correctly identify juvenile Pacific salmon species. The crew for each

electrofishing pass consisted of one electrofishing unit operator, two netters, and a bucket holder.

2.3.4 Data analyses

2.3.4.1 Fish abundance and density estimation

Estimates of juvenile salmon abundance were calculated using maximum-likelihood methods under the assumptions of the generalized-removal model (Otis et al. 1978). This model assumes that catches decrease with each pass, and that abundance may be estimated by the rate of decrease in catches between passes (i.e., depletion). In our study, depletions sometimes did not occur or were not large enough in successive sampling occasions (i.e., electrofishing passes) to use the generalized-removal model for abundance estimation. Estimates from these units were considered to be in violation of the removal-model assumptions and were not used to calculate average density values. To determine depletion failures, we used the depletion failure criterion of Otis et al. (1978) where for any value of first capture occasion, k, the criterion was (Equation 2.1):

$$\sum_{i=k}^{t}(t + k - 2i)u_i \leq 0 \quad , \tag{2.1}$$

where there were $i = 1, \ldots, t$ sampling occasions and u_j was the number of fish captured on the jth occasion..

2.3.4.2 Habitat unit area and density calculation

Juvenile salmon densities in each unit were calculated by dividing the removal-abundance estimates by the area of each unit sampled. The surface area ($\hat{a}_i$) of each unit was calculated by summing the four trapezoidal areas formed by the widths of the unit boundaries and transects (w_b) and the thalweg length (l; Equation 2.2; Figure 2.3C):

$$\hat{a}_i = \sum_{b=1}^{4} \frac{l}{4} \times \left(\frac{w_b + w_{b+1}}{2} \right) \quad . \tag{2.2}$$

Estimated densities in each unit ($\hat{d}_i$) were calculated by dividing the abundance estimate from the removal model ($\hat{N}$) in each unit by its area. These quantities were averaged to compute estimated mean density ($\hat{\bar{d}}$) separately for each species, study area and habitat-class stratum.

2.3.4.3 Data transformations

Proportional cover by overhanging vegetation (OHV), large woody debris (LWD), and undercut banks (UCB) were arcsine-square root transformed to normalize their distributions; all model coefficients for these variables were back-transformed to the proportion scale (i.e., values ranging from zero to one) for ease of interpretation. Frequency distributions and normal probability density curves for coho and sockeye salmon density, as well as for each habitat variable by study area, were checked for approximate normality (i.e., absence of kurtosis or skewness). Frequency distributions of coho and sockeye salmon density were negatively skewed (Figure 2.4). All habitat variable distributions were approximately normal with negative skewness observed among the distributions of OHV, UCB, and velocity (Figure 2.5). Multicollinearity was diagnosed ($r^2 > 0.3$) by examining pairwise regression plots of predictor variables and was not observed. To reduce redundancy in particle size variables, percent substrate by class in each habitat unit was converted to a particle size index (PSI) value according to the formula (Equation 2.3):

$$\text{PSI} = Log_e\left(\sum_{p=1}^{q}\frac{n_p}{n_q}\times m_p\right), \tag{2.3}$$

where n_p, the number of particles of the pth size class counted in a habitat unit, was divided by the number of particles of all q size classes to calculate the proportion of particles belonging to each size class. Each proportion of particle size p was then multiplied by m_p, the median value of the pth size class. The $\log_e$ of the sum of the

values was taken to normalize the disproportionate weight of the largest size classes on PSI.

2.3.4.4 Regression model building and model averaging

Juvenile salmon density was modeled as a function of proportional area of cover (OHV, LWD, and UCB) and hydraulic variables (depth, velocity, and particle size index) using generalized-linear modeling methods. One candidate set of regression models was selected for coho salmon density: a general model containing in-stream cover variables, hydraulic variables, and an intercept, an intercept-only model, one additive model each for combinations of three variables, and six models each containing one predictor variable and an intercept. Due to prohibitively small sample sizes, the sockeye salmon candidate model set contained only a general model, an intercept-only model, and one model for each predictor variable. The basic linear regression model formula was used:

$$\hat{d}_i = \alpha + \beta_1(X_1) + \beta_2(X_2) + \beta_3(X_3) + \beta_4(X_4) + \beta_5(X_5) + \beta_6(X_6), \quad (2.4)$$

where $\hat{d}_i$ was the density of species i, α was the intercept, X_1 was the proportional habitat unit area of overhanging vegetation, X_2 was the proportional habitat unit area of large woody debris, X_3 was the proportional habitat unit area of undercut banks, X_4 was the mean habitat unit depth, X_5 was the mean habitat unit velocity, and X_6 was the PSI value.

Parameter estimates (i.e., model coefficients α and β) were generated under each candidate model using the generalized-linear model function in R statistical software ("glm" function; R Development Core Team 2009). This function is a generalized-linear modeling algorithm that allows user specification of the distribution family of the response variable and corresponding link function, and uses an iteratively reweighted least squares method for maximum-likelihood estimation of the model parameters. The distribution family of the candidate model set was assumed to be Gaussian using the identity link.

An information-theoretic approach was used for model selection and model averaging of parameter estimates. Akaike's information criterion adjusted for small sample sizes (AIC_c) was used to identify a plausible set of R models from the set of

candidate models (Hurvich and Tsai 1989). This was accomplished by including in the plausible set those models whose delta AIC_c (Δ_i) values were less than the recommended value of eight (Burnham and Anderson 2010). Delta AIC_c values are simply the difference in AIC_c between the *i*th model and the AIC_c-selected "best" model. Once a set of plausible models was defined, parameter estimates ($\hat{\bar{\beta}}_j$; Equation 2.5a) of the *j* predictor variables under each plausible model *i* were averaged according to their Akaike weights (w_i; hereafter "weights"; Equation 2.5b) and their relative variable importance weights ($w_{+(j)}$; Equation 2.5c):

$$\hat{\bar{\beta}}_j = \frac{\sum_{i=1}^{R} w_i I_j(g_i) \hat{\beta}_{i,j}}{w_{+(j)}}, \tag{2.5a}$$

where

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)}, \tag{2.5b}$$

$$w_{+(j)} = \sum_{i=1}^{R} w_i I_j(g_i), \tag{2.5c}$$

and

$$I_j(g_i) = \begin{cases} 1 \text{ if predictor } x_j \text{ is in model } g_i, \\ 0 \text{ otherwise.} \end{cases}$$

Weights sum to one and are interpreted as the relative probability that model *i* is the "best" model in the set. Relative variable importance weights indicate how substantial the weight of evidence for a particular variable is relative to that of the other variables in the plausible set.

Standard errors of parameter estimates were calculated using the unconditional variance estimator of Burnham and Anderson (2010). Due to small habitat unit sample

sizes, coho and sockeye salmon densities (n = 33 and 11, respectively) were pooled across habitat classes and study areas in order to fit a series of regression models.

2.4 Results

2.4.1 Relationships between density and physical habitat variables

Candidate and plausible model sets and AIC_c rankings, as well as parameter estimates for juvenile coho and sockeye salmon density models, are in Appendices A2 and A3, respectively. The AIC_c-averaged model (hereafter "averaged model") of coho salmon density was estimated as:

$$\hat{d}_{coho} = 0.62 + 0.89(OHV) + 0.14(LWD) + 0.70(UCB) - 1.45(Depth) - 2.45(Velocity) + 0.08(PSI),$$

where proportional area of overhanging cover (OHV), large woody debris (LWD), and undercut banks (UCB), and depth (m), velocity (m/s), and particle size index values (PSI; values from 1 to about 6) were predictor variables (Table 2.4). According to variable importance values, UCB, OHV, and velocity effects had the most support in the data (Table 2.4). The model-averaged intercept of 0.62 predicts positive densities of coho salmon as values of physical habitat variables approach zero. Although zero values for depth and velocity are not biologically possible, the sign of the model-averaged intercept suggests that coho salmon density would be positive in habitats with no cover, slow velocities, shallow depths, and fine substrates.

The averaged model of juvenile sockeye salmon density as a function of physical habitat variables was estimated as:

$$\hat{d}_{sockeye} = 1.04 + 0.74(OHV) + 0.97(LWD) + 0.02(UCB) - 0.52(Depth) - 1.67(Velocity) - 0.40(PSI).$$

The positive intercept for the AIC_c-averaged model suggests that sockeye salmon densities would be positive at low values of the physical habitat variables. The evidence for the intercept-only model was substantial, given that salmon densities were assumed to be affected by physical habitat variables ($w_{Intercept\ Only}$ = 0.25). It should be noted that

small sample sizes limited models to one predictor each and, as a result, it is difficult to determine whether additive effects of physical habitat variables influenced sockeye salmon densities in this study.

2.4.2 Effects of habitat variables on juvenile salmon density

In the averaged models, in-stream cover had strong positive effects on coho salmon (Figure 2.6) and sockeye salmon density (Figure 2.7). Undercut banks and OHV had the strongest positive effects on coho salmon density ($\hat{\bar{\beta}}_{UCB}$ and $\hat{\bar{\beta}}_{OHV}$ = 0.89 and 0.70, respectively), but the effect of LWD was small and largely unsupported ($\hat{\bar{\beta}}_{UCB}$ = 0.14; $w_{+(\mathrm{LWD})}$ = 0.06). Sockeye salmon density was positively related to OHV, LWD, and UCB ($\hat{\bar{\beta}}_{OHV}$, $\hat{\bar{\beta}}_{LWD}$, and $\hat{\bar{\beta}}_{UCB}$ = 0.74, 0.97, and 0.02, respectively). Although positive relationships between cover and density existed for coho and sockeye salmon, the evidence weights for cover effects differed between species. For coho salmon, effects of OHV and UCB were well supported ($w_{+(OHV)}$ and $w_{+(UCB)}$ = 0.89 and 1, respectively). By comparison, effects of OHV, LWD, and UCB on sockeye salmon density had little support ($w_{+(OHV)}$, $w_{+(LWD)}$, and $w_{+(UCB)}$ = 0.07, 0.03, and 0.05, respectively). These results suggest that cover affected coho salmon more than it did sockeye salmon.

In contrast to the similarity of cover effects, hydraulic variables had mixed effects on coho and sockeye salmon density. Velocity was negatively related to coho and sockeye salmon density ($\hat{\bar{\beta}}_{Velocity}$ = -2.45 and -1.67, respectively), and depth also had a negative, albeit smaller, negative effect on density ($\hat{\bar{\beta}}_{Depth}$ = -1.45 and -0.52, respectively). The relationship between density and velocity was well supported for coho salmon, but not for sockeye salmon ($w_{+(Velocity)}$ = 0.85 and 0.28, respectively). Conversely, the relationship between PSI and density had more support for sockeye salmon than for coho salmon ($w_{+(PSI)}$ = 0.29 and 0.02, respectively). The effects of PSI on density were positive and negative for coho ($\hat{\bar{\beta}}_{PSI}$ = 0.08) and sockeye salmon ($\hat{\bar{\beta}}_{PSI}$ = -0.40), respectively. Of the hydraulic variables, velocity had the strongest negative relationships with coho and sockeye salmon densities.

2.4.3 Goodness of averaged model fit

The averaged models of coho and sockeye salmon density fit their respective datasets poorly (Figure 2.8). The low R^2 value of the relationship between observed and predicted salmon densities suggests that other processes more strongly affected coho and sockeye salmon densities (R^2 = 0.28 and 0.35, respectively). The predictive abilities of the averaged models were also poor. Simple linear regression of observed coho and sockeye salmon densities versus model predictions showed positive relationships (slope = 0.62 and 0.18, respectively). Based on these results, predicted coho and sockeye salmon densities were on average 82% and 38% smaller than the observed densities, respectively.

2.5 Discussion

Densities of juvenile coho and sockeye salmon were positively related to proportional area of cover by overhanging vegetation (OHV), large woody debris (LWD), and undercut banks (UCB). These relationships, however, varied in terms of magnitude and weights of evidence in the averaged models. Negative effects depth and velocity on coho and sockeye salmon density were observed, while particle size was positively and negatively correlated with coho and sockeye salmon density, respectively. In general, the relationships among juvenile salmon populations and physical microhabitat features depict patterns in key individual behaviors, such as foraging and predator avoidance (Quinn 2005). The highest densities of juvenile salmon are often found in habitats that are most suitable for growth and offer refuge from predators, so long as those habitats are not limited in any other way (Nunn et al. 2012). My results, with few exceptions, fit into this framework of individual-to-group distribution, wherein individual behaviors affect habitat selection, which in turn affect the number of individuals in a given habitat.

2.5.1 Effects of in-stream cover on juvenile salmon density

In-stream cover had strong positive effects on coho salmon density, and positive effects of varying magnitude on sockeye salmon density. Associations between juvenile

salmon abundance and in-stream cover are ubiquitous in the literature (e.g., Quinn and Peterson 1996; Hauer et al. 1999; Rosenfeld et al. 2000; Mossop and Bradford 2004). Specifically, strong positive effects of OHV and UCB on coho salmon density were evident in our study. Overhanging vegetation and UCB have been shown to reduce predation on juvenile brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *O. mykiss* by terrestrial predators through visual isolation (Butler and Hawthorne 1968). In addition to direct effects, cover may also have indirect effects on juvenile coho salmon. Experiments by Dill and Fraser (1984) confirmed that perceived predation risk due to an absence of cover resulted in a decrease in net rate of energy intake and growth of juvenile coho salmon. Decreased growth during freshwater rearing is often linked to increased mortality during subsequent life stages (Parker 1968; Pearcy 1992). In contrast to coho salmon, support in the data for an effect of in-stream cover on sockeye salmon densities was marginal. The influence of cover has not been examined for stream-type sockeye salmon; however, lake-type sockeye salmon have been shown to migrate vertically within the water column to depths that minimize their risk of exposure to predators (Scheuerell and Schindler 2003). It may be possible that stream-type sockeye salmon have different avian predator avoidance strategies than coho salmon, which may explain why we failed to observe sockeye salmon using in-stream cover and why they frequently formed dense aggregations at the water surface (Hoar 1954; J. Coleman, UAF, personal observation). Because sockeye salmon do not actively defend feeding positions or associate with fixed structures, we surmised that cover may not be important for predator avoidance. Instead, sockeye salmon may be exhibiting risk dilution or predator inspection behaviors by aggregating in the presence of potential predators (Pitcher 1992).

2.5.2 Effects of hydraulic variables on juvenile salmon density

Coho and sockeye salmon densities in this study were negatively related to velocity. In stream environments, responses of juvenile salmon to velocity are typically associated with individual foraging behaviors. Beecher et al. (2002) found that juvenile coho salmon preferred a very narrow range of stream velocities (3 to 6 $cm \cdot s^{-1}$) and avoided velocities greater than 55 $cm \cdot s^{-1}$. This range highlights the trade-off between

maximizing prey encounter rate and minimizing energy expenditure for maintaining a constant stream position (Nielsen 1992). In addition to individual behavior, reach-scale habitat factors have also been cited as drivers of juvenile salmon density. Sharma and Hilborn (2001) reported a decline in the number of coho salmon smolts produced per km of stream with increasing stream gradient (i.e., higher velocities), and increased smolt production with increased area of low-velocity habitats. In contrast, Seiler et al. (2002) found that the number of smolts produced per year in a Washington stream was positively related to average summer discharge. This relationship can occur in systems where habitats regularly become disconnected due to periods of extremely low velocity, but this was not the case in this study. Although the precise reason is unknown, it is evident from these results and from those of similar studies that fish densities are higher in low-velocity habitats during summer rearing than their high-velocity counterparts.

Coho and sockeye salmon densities were also negatively related to depth. Juvenile salmon have been shown to select areas that maximize foraging success and minimize predation risk in the stream environment (Bustard and Narver 1975; Beecher et al. 2002). In several studies of habitat use, coho salmon showed preferences for depths of 0.5 to 1.2 m during summer rearing periods (Ruggles 1966; Lonzarich and Quinn 1995; Bugert et al. 1991). In this study, deeper habitat units had lower fish densities, which may be attributed to higher predation risk by adult fish without the benefit of increased foraging success at lower depths. Research on depth preferences of sockeye salmon has focused exclusively on lake-rearing populations, but may have some applicability to the stream environment. In lakes, sockeye salmon are sight predators and typically feed on zooplankton and aquatic invertebrates (Quinn 2005). Scheuerell and Schindler (2003) found that juvenile sockeye salmon migrated vertically within the water column and that the depths they moved to provided sufficient light intensity for foraging by sight while minimizing visual exposure to predators. It is plausible that sockeye salmon in streams use the same mechanisms, and that increased depth equates to decreased light intensity for profitable foraging in lotic systems (Clark and Levy 1988).

The effect of particle size on juvenile salmon density was less consistent than either depth or velocity. Evidence existed for a weak positive effect of particle size on coho salmon density. In clear-water streams where suspended sediment is low, small particle sizes are unlikely to affect juvenile salmon density (Bjornn and Reiser 1991). However, previous research has shown a preference by stream-dwelling salmonids for habitats with gravel or larger substrates that provide spaces for avoidance of high velocities and predators (Tiffan et al. 2006; Naguyama and Nakamura 2007). Additionally, high levels of suspended sediment also create low-visibility conditions in which drift feeding or active foraging is less profitable. Berg and Northcote (1985) exposed juvenile coho salmon to turbidity levels up to 60 NTU for up to 4.5 days, which disrupted territoriality and feeding behaviors. However, the effect of particle size on juvenile coho salmon density in this study was weak, and so individual responses to particle size are relatively unimportant in this system.

In contrast to coho salmon, we observed a moderate negative effect of particle size on sockeye salmon density. Based on the regression model, densities would be expected to be higher in habitat units with smaller particle sizes. This may be because prey items favored by sockeye salmon select habitats with fine sediments and macrophyte growth (Grenouillet et al. 2001). Similarly, Edmundson and Mazumder (2001) found that zooplankton density was the best predictor of juvenile salmon growth in Alaskan lakes. Off-channel areas with sand or silt sediments are similar to lake shorelines, which are profitable foraging areas for visual feeders in terms of prey availability and foraging success (Rogers 1973). It is possible that stream-type sockeye salmon have adopted drift-feeding behaviors; however, the differences observed between coho and sockeye salmon responses to decreasing particle size suggests that they may differ in their feeding behaviors. The negative relationship between sockeye salmon density and particle size may be unrelated to foraging, but determining causal mechanisms of this pattern will require further study.

2.5.3 Limitations and future study

Although clear patterns were described between juvenile salmon density and physical habitat variables, caution must be used when applying these results outside the context of this study for several reasons. First, the physical characteristics of freshwater habitats tend to differ across small spatial scales and geomorphic gradients (e.g., river length and complexity, elevation, valley confinement). This is especially true of the rivers in Bristol Bay, which is precisely why such a high diversity of life-history patterns exists among salmon stocks in this drainage. Examples of the unique freshwater habitats found in Bristol Bay include deep "fjord lakes" with inlets, outlets, sand bars and beaches, shallow-grade coastal rivers, and off-channel floodplain ponds, to which hundreds of resident spawning stocks are finely adapted (Manley et al. 2001; McPhee et al. 2009; Gomez-Uchida et al. 2011). Maintaining the diversity of freshwater habitats is essential to protecting the diversity of salmon in the Bristol Bay region, but managers must use caution when generalizing fish-habitat relationships across watersheds.

In addition to limitations imposed by the geographic scope of this study, the three-week sampling period used did not encompass any temporal variability in fish-habitat relationships, which can vary widely across years in response to environmental or demographic factors (Peterson 1982; Lonzarich et al. 2009; Reeves et al. 2011). In a study of juvenile sockeye salmon in Lake Aleknagik, Alaska, Rogers (1973) reported no correlation in annual abundance over a ten-year period. In addition to variability between years, juvenile salmon density varies across a single growing season. In many subarctic rearing lakes and streams, abundances increase until early August, then decrease sharply through the fall (Niemelä et al. 2001; Bryant et al. 2004). My results characterize short-term summer rearing patterns of juvenile coho and sockeye salmon and therefore can only suggest what effects changes in physical habitat may have on fish densities and inform future research. Repeated sampling, including multiple sampling periods within and across years, is essential to fully understanding the dynamic relationships between stream-rearing fish and their habitats.

Investigating the physical aspects of habitat are but one of many approaches to quantifying fish-habitat relationships. The intercepts of the averaged regression models were positive for both coho and sockeye salmon, indicating that if all of the physical habitat variable values in a unit equaled zero, the models predicted fish densities greater than zero. A non-zero intercept suggests extrapolation of the regression model fit beyond the range of data observed (Guthery and Bingham 2007). In the present study, this could equate to extrapolation of density predictions beyond physical habitat variable values of zero (i.e., negative), and would account for a non-zero intercept. It is also possible that accurate prediction of juvenile salmon density is not solely a function of physical variables. Other abiotic (e.g., water chemistry, dissolved oxygen concentration) or biotic (e.g., prey density and availability, predator density, intra- or interspecific competition) predictor variables may explain positive fish densities when physical habitat variables are theoretically zero.

Relating our observations to those from previous studies on juvenile salmon was challenging because co-occurring stream-type sockeye and coho salmon in southwestern Alaska have not been described (but see Rice et al. 1994 for discussion of stream-type sockeye salmon in southeast Alaska). In addition, our study is the first to quantify relationships between in-stream habitat characteristics and stream-rearing sockeye salmon. The origins of the stream-type life history are not fully understood, but research by McPhee et al. (2009) suggests that lake-type sockeye salmon populations formed via straying from principal colonizing populations in southwestern Alaska streams. Knowing how and when different salmon life-history types diverged is critical to our understanding of their individual behaviors and population-level habitat use. Additional studies of stream-rearing sockeye salmon are needed to corroborate the findings presented in this research and to further our knowledge of their habitat requirements.

The most important limitation of our study was the small number of habitat units with reliable estimates of coho and sockeye salmon density. Consequently, data needed to be pooled in order to use regression methods, which meant incorporating known variability between study areas and habitat classes in both density estimates and habitat

variable values. Including this extra variability in the regression models may have obscured some effects and inflated others; however, the effects identified here were largely in agreement with findings from numerous studies of juvenile salmon habitat use. As in many observational studies in remote areas, high travel costs reduced the amount of time we were able to spend in the field, and as a result, the number of habitat units sampled was limited. To reduce the amount of time needed at each sampling site, fish capture methods that are less intensive than electrofishing and better suited to different habitat types should be used (i.e., minnow traps that can be left overnight and used in soft sediments). In addition to increasing cost efficiency, using alternative or multiple gear types has the advantage of providing more accurate estimates of fish density than removal electrofishing alone (Peterson et al. 2004; Rosenberger and Dunham 2005; Carrier et al. 2009). Exploring the sampling techniques and study designs that deliver cost-efficient and accurate estimates of salmon-habitat relationships is essential to long-term monitoring of stream-rearing salmon.

2.5.4 Conclusion

My study showed that in-stream cover is positively correlated with juvenile salmon density, and water depth and velocity are negatively correlated with density. We observed weak positive and negative relationships between substrate size and coho and sockeye salmon density, respectively. From these results, we concluded that although sockeye salmon and coho salmon co-occurred in nearly all of the study sites, they established different patterns of physical habitat use. Whether these differences were due to behavioral adaptations (e.g., foraging, predator avoidance) or other factors, they are examples of how sympatric species use freshwater habitat and emphasize the importance of maintaining the diversity of freshwater habitats in Bristol Bay.

Information about the habitat relationships that characterize Pacific salmon is lacking in many Alaskan rivers. This dearth is due to the high cost of obtaining information and the absence of large-scale landscape change that has plagued much of the salmon habitat elsewhere in North America. However, as resource development and other anthropogenic impacts become commonplace in pristine salmon habitats such as

Bristol Bay, and as climate change continues to restructure stream communities, having insufficient data on salmon-habitat relationships will become increasingly problematic. Managers need data to make informed decisions about land use that take into account the potential threats to stream-rearing fish and their critical habitats. The fish-habitat relationships described by this study can inform fishery and land-use decisions in the Bristol Bay region, and, when collected over long time periods, they exemplify the type information required to ensure the sustainability of freshwater ecosystems.

Table 2.1. Classification scheme described by Marcus (2002) and Marcus et al. (2003), adapted from Bisson et al. (1982).

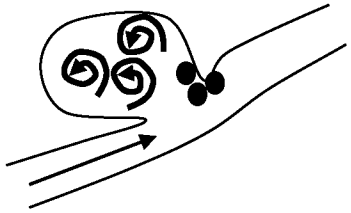
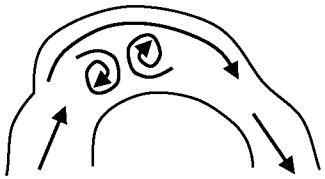
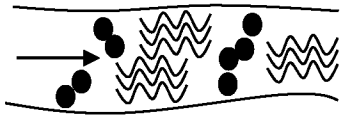
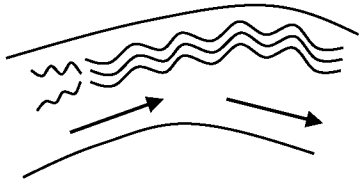
Habitat class	Description	Schematic
Eddy drop zones (EDZ)	Areas of low surface turbulence where backwater circulation deposits fine grained sediments; often peripherally attached to main channel	
Pools	Areas that display little surface disturbance and are usually 0.7 m or more in depth; may be scours located at channel bends	
Riffles	Shallow areas which display significant surface riffles and have slopes of 1-2% in the study area	
Runs	Areas of shallow, smooth flow with coarse gravel substrates (glides) or areas that are deeper and slightly more turbulent with a definite thalweg (runs)	

Table 2.2. Descriptions of physical habitat variables measured in habitat units and used as predictors in juvenile salmon density regression models.

Habitat variable	Units and description
Class	Categories: pool, riffle, glide, eddy drop zone
Substrate composition	Percent substrata by class
LWD	m^2; mapped onto imagery and length and width measured
Wetted width	m; measured at ¼, ½, and ¾ points perpendicular to thalweg
Thalweg length	m
Depth	m; measured at nine points in each unit
Velocity	$m \cdot s^{-1}$; measured at nine points in each unit
Water temperature	°C; measured at one point in each unit

Table 2.3. Categorical classes used for measuring substrate compositions.

Substrate class	Median axis size range (mm)
Fines	< 2
Small gravel	2–8
Gravel	8–64
Small cobble	64–128
Cobble	128–256
Small boulder	256–512
Boulder	>512
Bedrock	Solid rock

Table 2.4. Predictor variables and relative variable importance weights (in parentheses; see equation 2.4 in text) for AIC_c-averaged regression models of coho and sockeye salmon density versus physical habitat. Fish and habitat were surveyed in the Kulukak River using electrofishing and stream assessment methods, respectively, in July 2010.

Species	Intercept	OHV	LWD	UCB	Depth	Velocity	PSI
Coho	0.62	0.89	0.14	0.70	-1.45	-2.45	0.08
	(1)	(0.89)	(0.06)	(1)	(0.02)	(0.85)	(0.02)
Sockeye	1.04	0.74	0.97	0.02	-0.52	-1.67	-0.40
	(1)	(0.07)	(0.03)	(0.05)	(0.03)	(0.28)	(0.29)

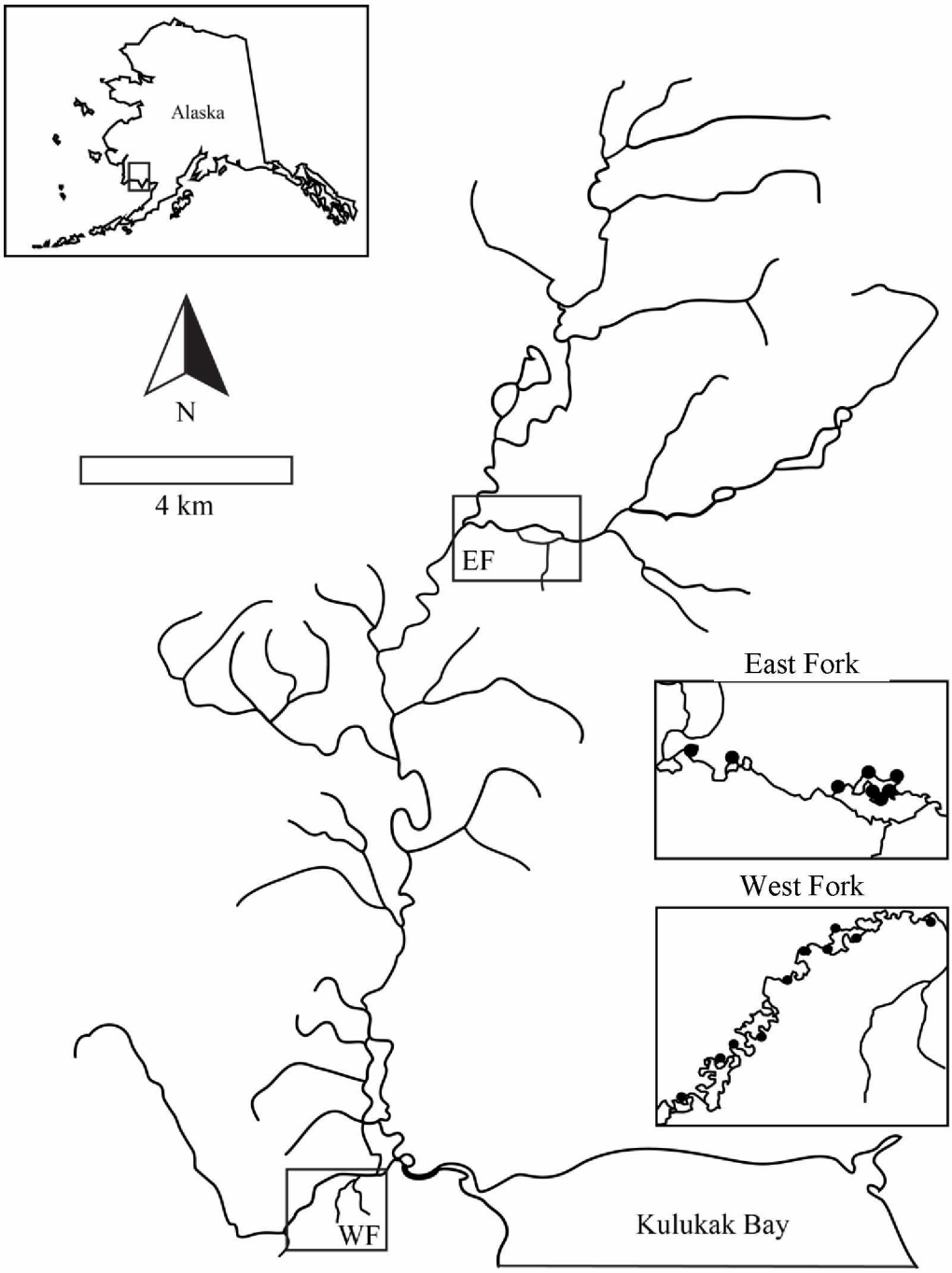


Figure 2.1. Map of study site. The main map shows the Kulukak River and its location in Alaska (upper left inset map). The detailed maps on the right show the 100-m reaches that were selected (dots) for fish surveys and habitat inventories in each study area. Figure adapted from MacDonald (1996).

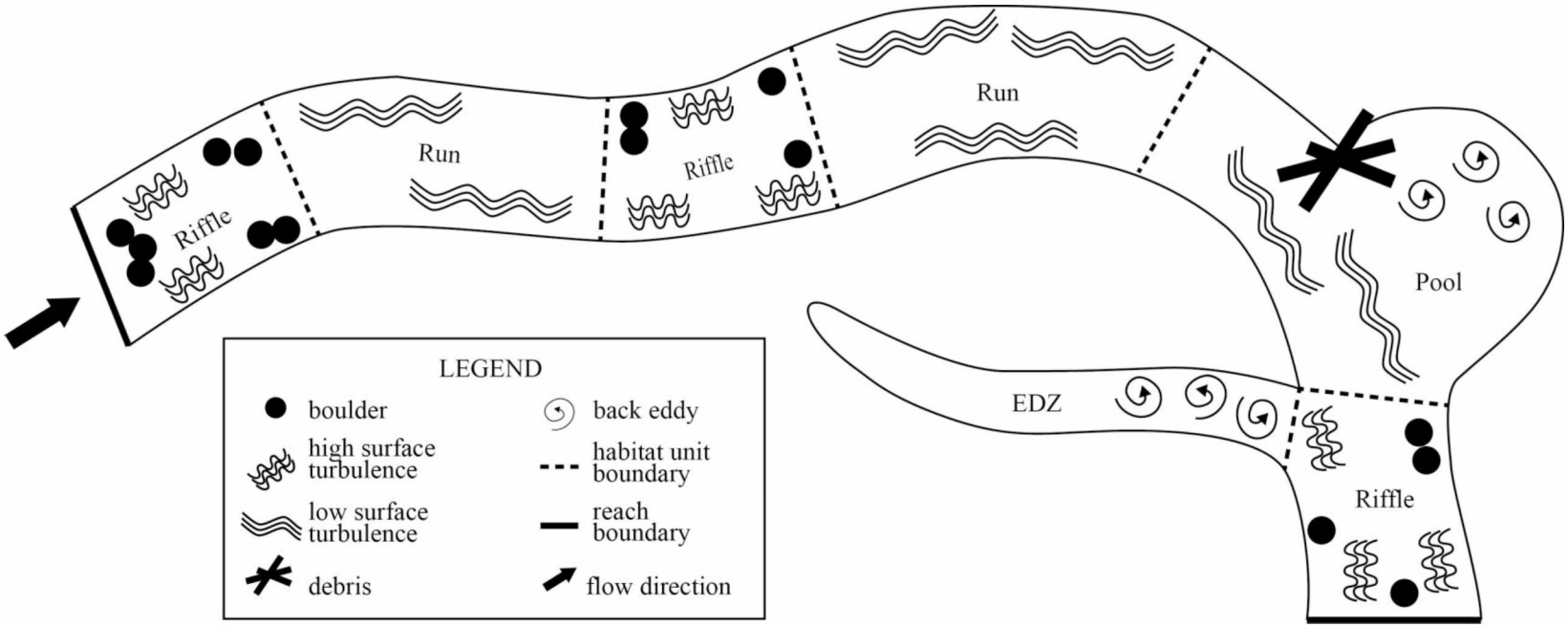


Figure 2.2. Schematic of fish survey and habitat inventory sample reach. In the hypothetical sample reach pictured, the units classified as pool and eddy drop zone (EDZ) habitat would be sampled. Because multiple riffles and runs are located within the sample reach, only one riffle and one run would be randomly selected for habitat measurements and removal electrofishing.

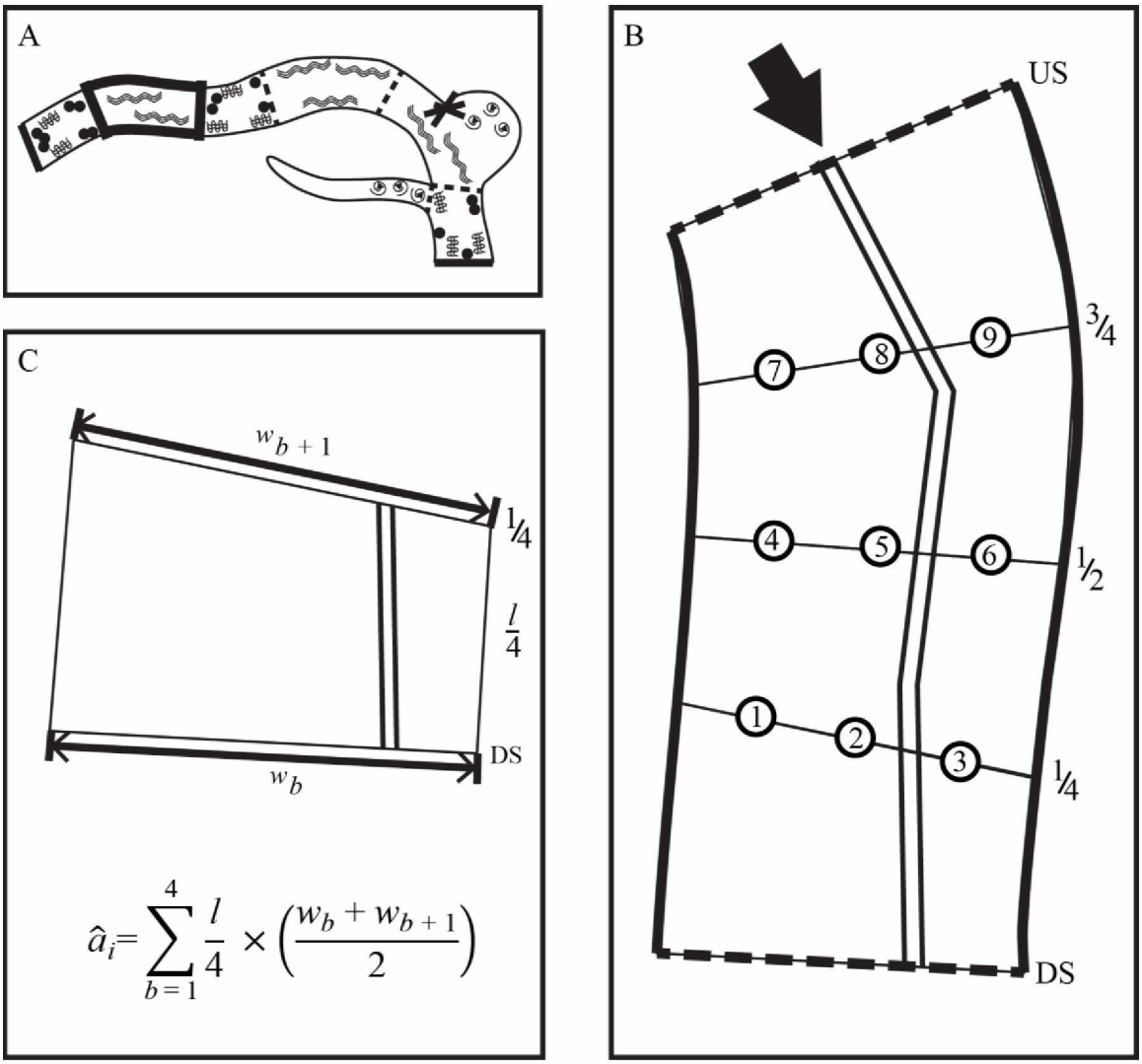


Figure 2.3. Schematic of sample reach (A), habitat unit (B), and habitat unit section and area measurements (C). Panel (A) shows a hypothetical reach with one habitat unit outlined in black. Panel (B) shows the unit thalweg, upstream (US) and downstream (DS) boundaries, flow direction represented by the double black line, dashed line, and black arrow, respectively. Circled numbers represent locations where depth and velocity measurements were taken on ¼, ½, and ¾ transects. Panel (C) shows width and length measurements and equation used to calculate habitat unit area.

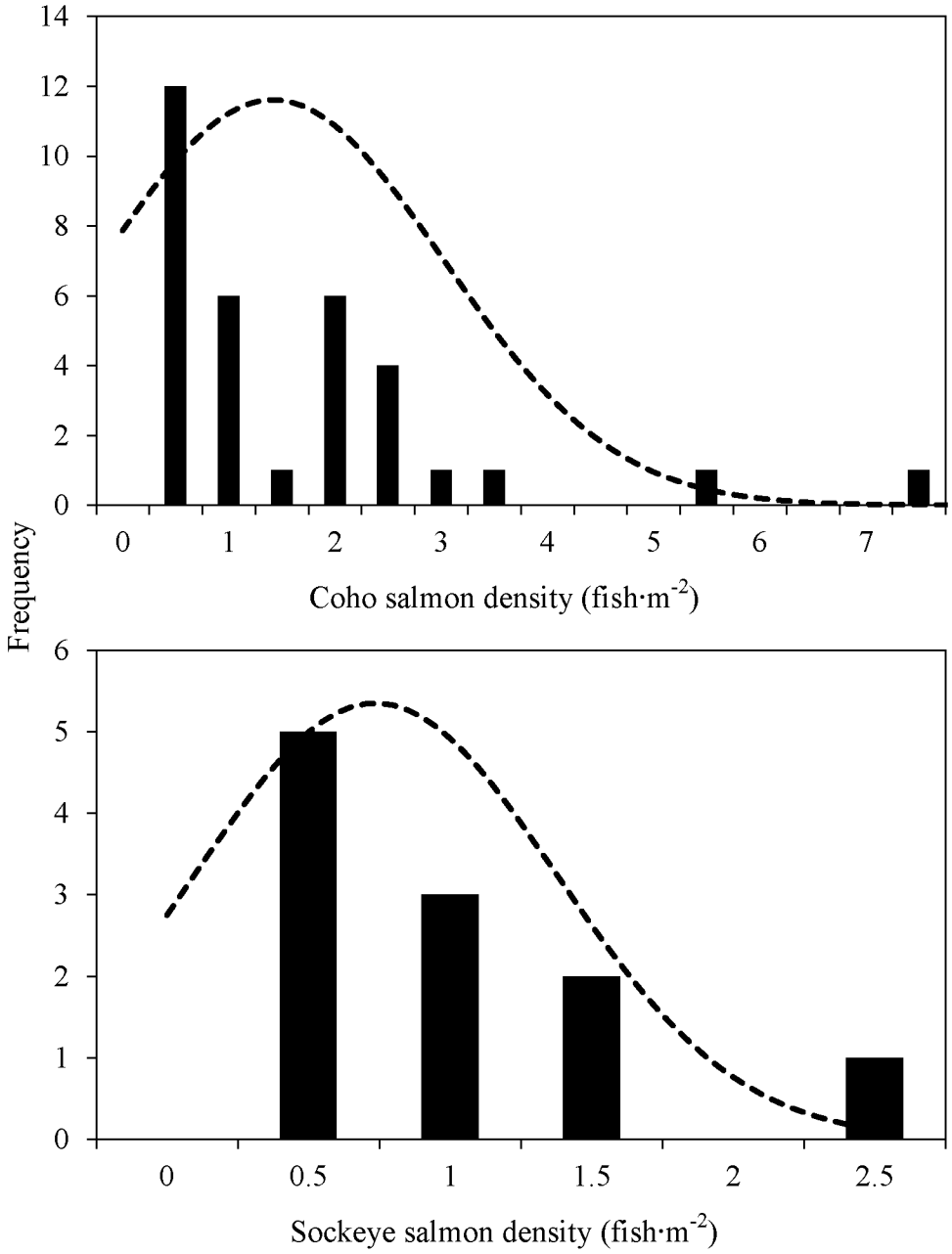


Figure 2.4. Frequency distributions of juvenile salmon density (fish·m^{-2}; coho [top panel] and sockeye salmon [bottom panel]). Normal distribution probability density curves are overlaid (dashed line) for comparison with frequency distributions.

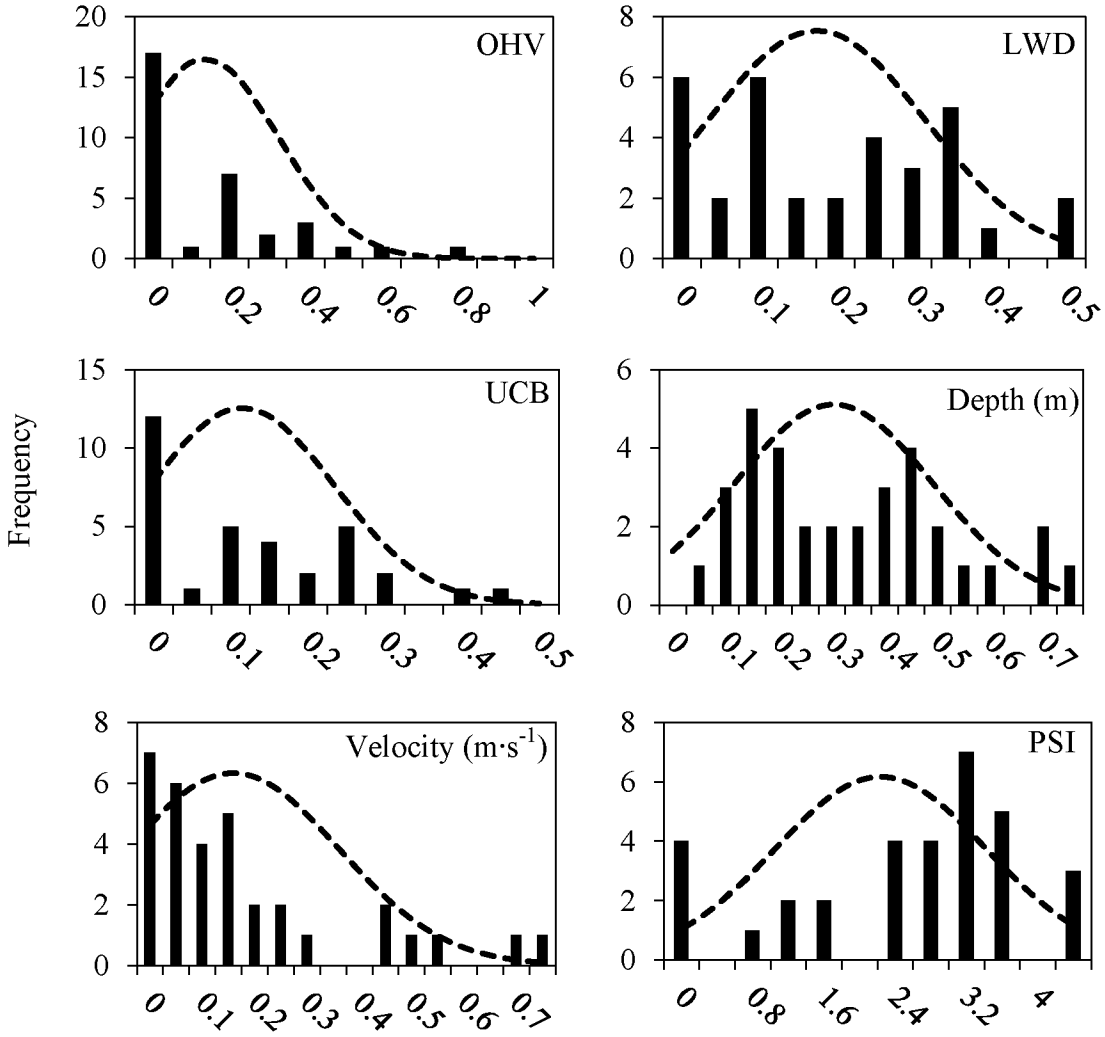


Figure 2.5. Frequency distributions of proportional cover by overhanging vegetation (OHV; top left), large woody debris (LWD; top right), undercut banks (UCB; middle left), depth (middle right), velocity (bottom left), and particle size index (PSI; bottom right; see equation 2.3 in text for calculation of PSI values). Normal distribution probability density curves are overlaid (dashed line) for comparison with frequency distributions. Habitat variables were measured in a random sample of habitat units in the Kulukak River in July 2010.

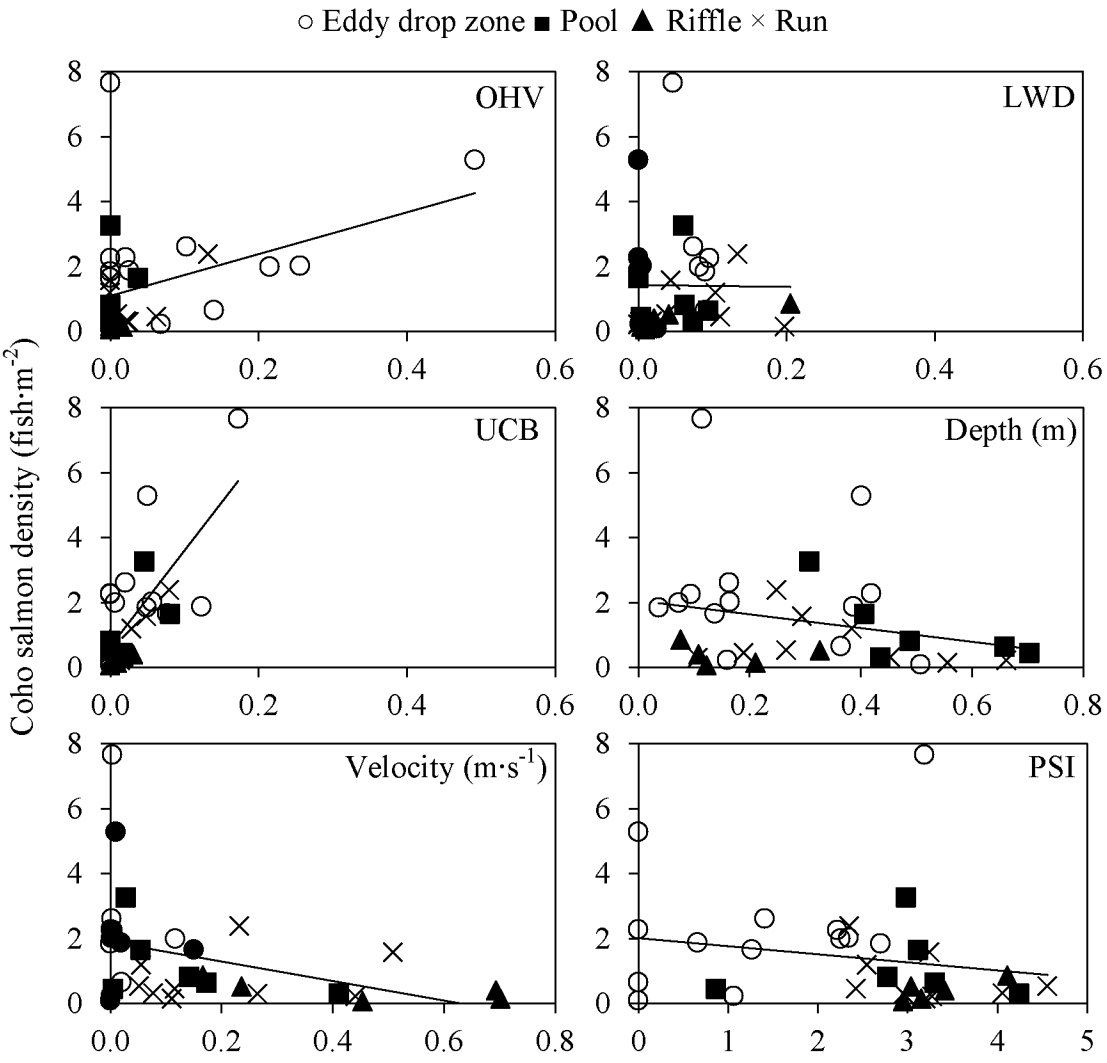


Figure 2.6. Coho salmon density (fish·m^{-2}) versus proportional area of cover by overhanging vegetation (OHV; top left), large woody debris (LWD; top right), undercut banks (UCB; middle left); depth (middle right), velocity (bottom left), and particle size index (PSI; bottom right; see equation 2.3 in text for calculation of PSI values). Lines represent simple linear regressions. Habitat variables were measured in a random sample of habitat units (n = 33) in the Kulukak River in July 2010.

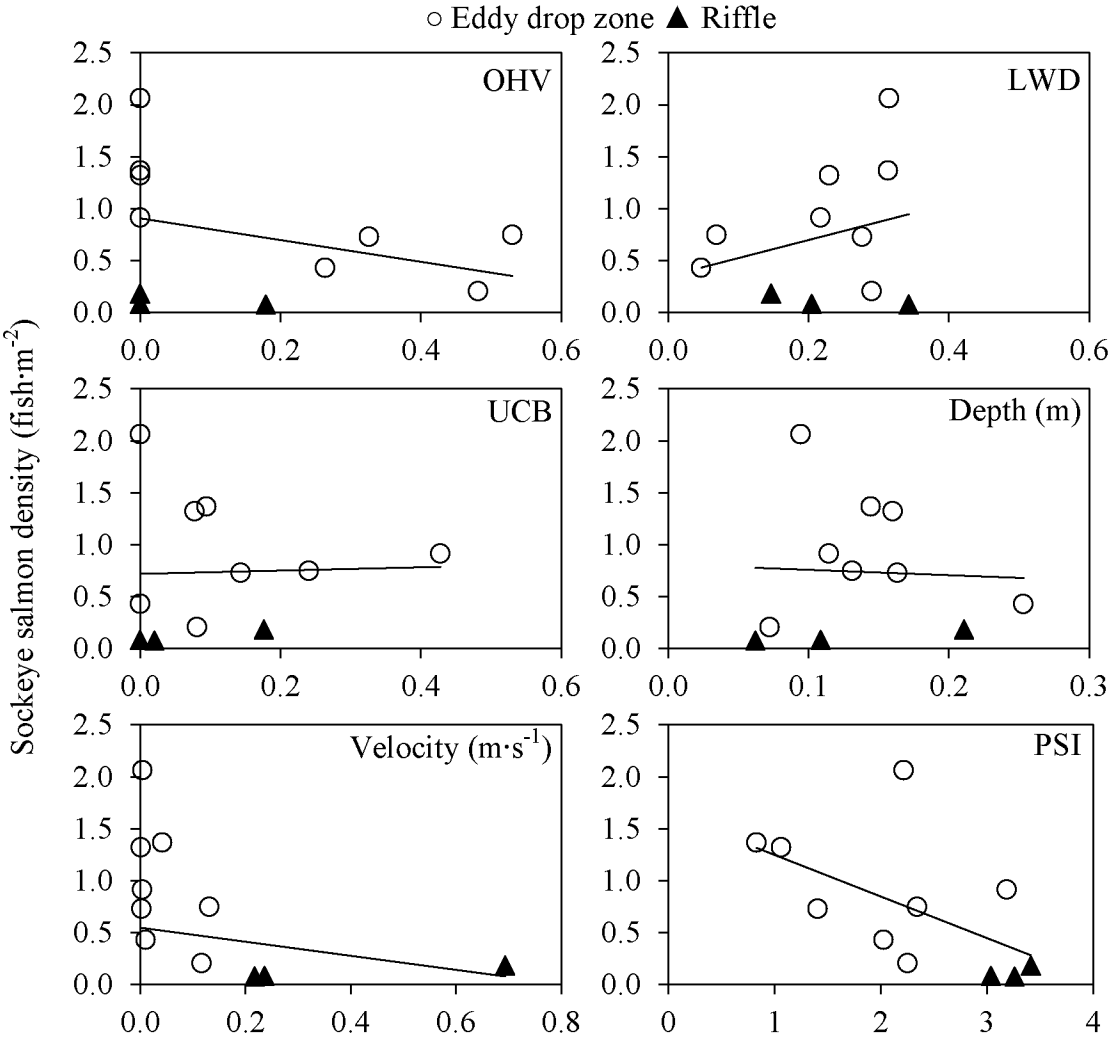


Figure 2.7. Sockeye salmon density (fish·m^{-2}) versus proportional area of cover by overhanging vegetation (OHV; top left), large woody debris (LWD; top right), undercut banks (UCB; middle left); depth (middle right), velocity (bottom left), and particle size index (PSI; bottom right; see equation 2.3 in text for calculation of PSI values). Lines represent simple linear regressions. Habitat variables were measured in a random sample of habitat units (n = 11) in the Kulukak River in July 2010.

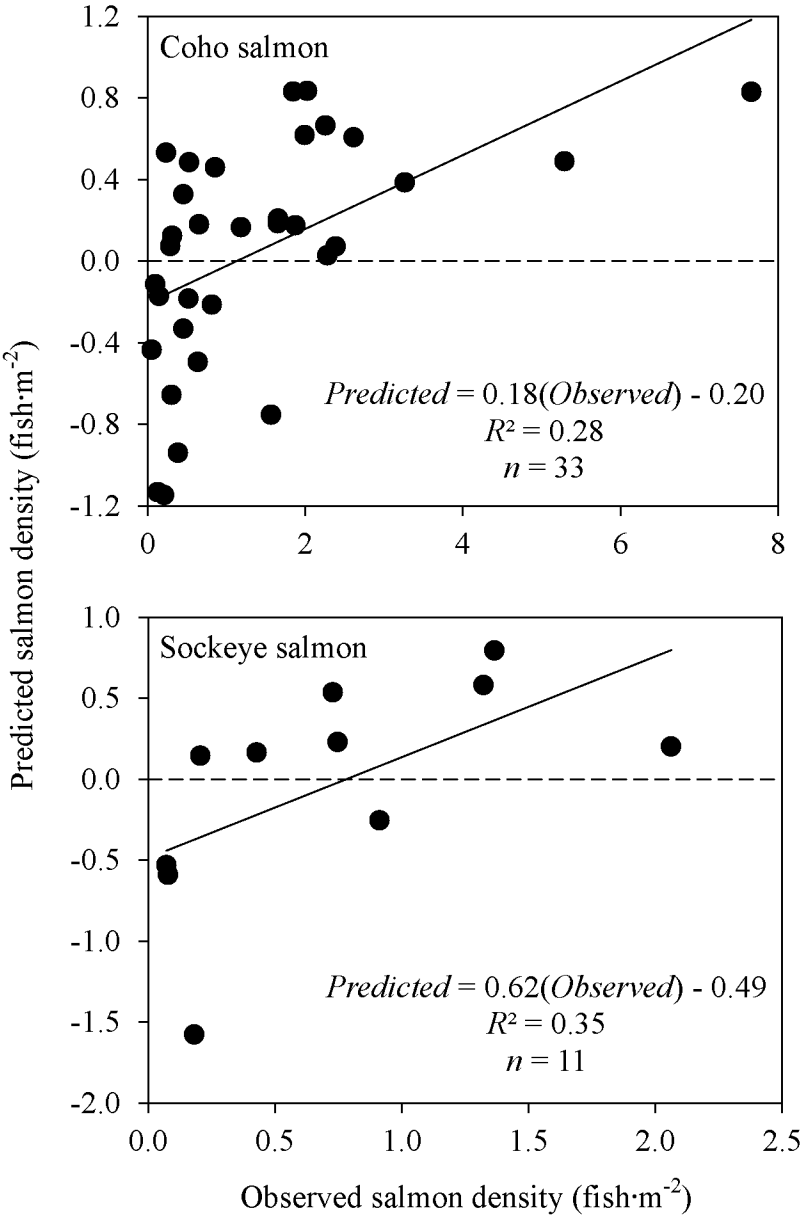


Figure 2.8. Observed versus predicted coho (top panel) and sockeye (bottom panel) salmon densities (fish·m^{-2}). Model predictions were based on AIC_c-averaged model coefficients and observed habitat variable values. Solid lines and equations represent simple linear regression; dashed lines show $Y = 0$ line for reference.

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Conclusions

My study was the first step in establishing a freshwater habitat and juvenile salmon abundance monitoring program on Togiak National Wildlife Refuge lands in Bristol Bay, Alaska. In chapter one, I established baseline estimates of juvenile coho and sockeye salmon abundance and freshwater habitat quantity in two study areas of the Kulukak River. Eddy drop zones comprised a third of the available freshwater habitat in the study areas, were heavily used by both coho and sockeye salmon, and were determined to be important habitats for salmon during summer rearing. The results of the second objective are useful as baseline estimates of the correlations between juvenile salmon and their rearing habitats. Specifically, in-stream cover was positively correlated with juvenile salmon density, with undercut banks and large woody debris having the strongest effects on coho and sockeye salmon density, respectively. Depth and velocity were both negatively correlated with density, and sockeye salmon density was negatively related to substrate size. The quantitative estimates of juvenile Pacific salmon density, habitat area, and fish-habitat relationships we have described are valuable to increasing our knowledge of the dynamics of coho and sockeye salmon stocks for understanding of climate- and landscape-change effects not only in Alaska, but throughout their range.

Many of the world's Pacific salmon stocks inhabit waters adjacent to human-altered landscapes. In ecosystems with dense human populations such as the Columbia River basin in the northwestern United States, landscape changes have devastated salmon habitat (Williams et al. 1991; Reeves et al. 1993; NRC 1996). In many others, however, the implications of fish habitat alterations resulting from urban development, logging, mining, and hydropower projects are unknown. Some of the effects on freshwater salmon habitat that have been documented in degraded ecosystems include reduced large wood input from logged riparian zones (Murphy and Hall 1981; Hauer et al. 1999; Scheurer et al. 2009), habitat fragmentation and altered flow regimes from hydropower dams (Poff et al. 1997; Freeman et al. 2001), and physical destruction and dewatering of in-stream habitats for infrastructure and road building (Platts et al. 1989; Espinosa et al. 1997). If data on the fish-habitat relationships in the Columbia River system had been available

before extensive habitat alteration occurred, it might have been possible to recognize changes in salmon productivity early on. In relatively pristine landscapes, such as Bristol Bay, mitigation of habitat alteration effects on salmon stocks through fish and habitat assessment and monitoring is still possible.

Although many of the world's Pacific salmon fisheries are not threatened by human-caused landscape alteration, none are immune to changes induced by global climatic shifts. While the changes predicted for individual fisheries are too complex to illustrate here, it is proposed that the freshwater habitats currently available to salmon will change in location, quantity, and quality (but see Ficke et al. 2007 for a review of climate change effects on freshwater fisheries). Generally, warmer air temperatures will lead to warmer water temperatures, fewer flood events, and reduced stream discharge during summer months (Rouse et al. 1997; Wigley 1999; Poff et al. 2002; Walsh et al. 2005). These trends will have secondary impacts on salmon rearing habitat quality; including reduced deposition of in-stream wood, changes in riparian vegetation communities and reduced overhanging plant cover, reduced water depth and velocity, and increased deposition of fine sediments (Beamish and Bouillon 1993; Meyer et al. 1999; Battin et al. 2007; Merritt et al. 2010). Rather than speculate on the net effects of these impacts, however, researchers should focus on establishing reference points against which future scenarios of climate and landscape change may be compared.

Recognition of climate and landscape effects must be followed by mitigatory actions on the part of land-use and fishery managers. Potential actions include: (1) reducing land and water-use activities that hinder hydrologic processes regulating natural stream discharge, sediment and LWD deposition, and formation of pool habitats and undercut banks (Mantua et al. 2010), (2) protecting off-channel habitats that provide refuge for juvenile salmon from high water velocities, (3) protecting riparian zones that supply in-stream wood and overhead vegetative cover that are valuable refuges from predators and feeding sites, and (4) restrict to non-fish-bearing streams any practices that have been shown to be destructive to in-stream habitats (e.g., road building, dewatering,

damming). Specific actions will depend on the inherent fish-habitat relationships and variability of the ecosystem and the proposed or predicted landscape changes in question.

This study served as an example of the baseline data necessary to examine climate- and human-induced changes in the fish-habitat linkages in freshwater ecosystems (Day et al. 2008). Although this research was conducted in southwestern Alaska, the methods used are widely applicable to small river systems throughout the geographical range of Pacific salmon. Baseline data, along with continued monitoring of fish populations and their habitats, are essential to understanding the effects of change and to making well-informed, responsive decisions about land use and habitat conservation.

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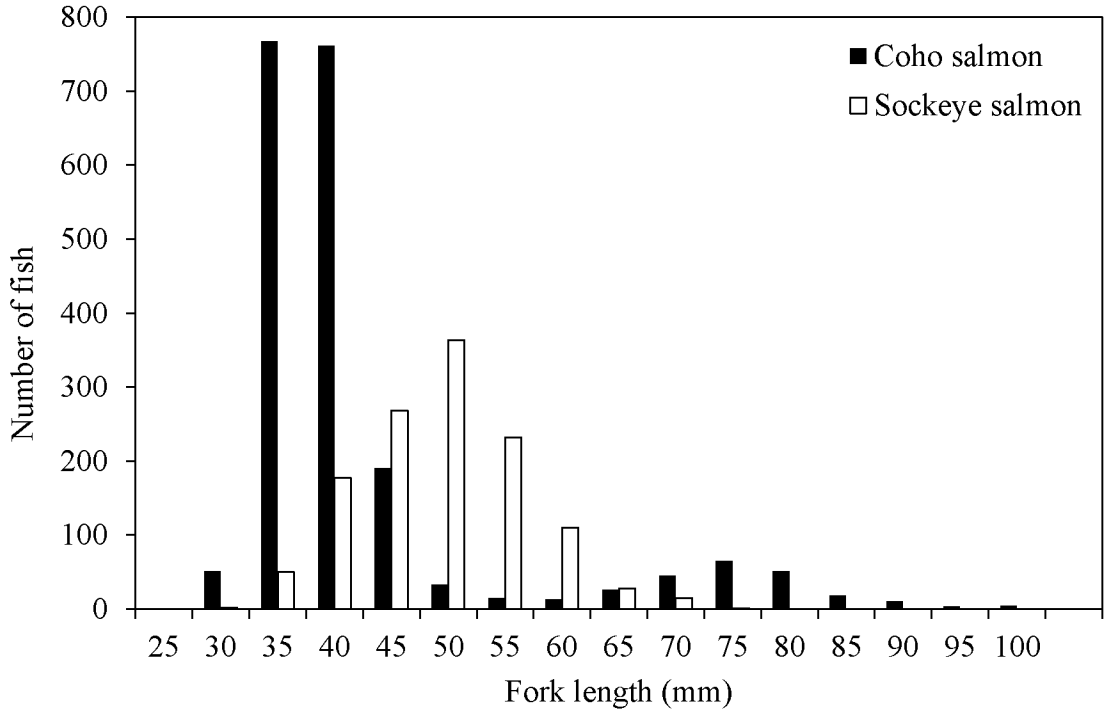

Appendix A1. Length-frequency histogram of coho and sockeye salmon fork lengths (mm). All fish were measured during four-pass depletion sampling in July 2010.

Appendix A2. Plausible removal-model sets of juvenile coho and sockeye salmon by habitat class and study area stratum. Removal models were fitted to capture histories of juvenile coho salmon sampled using four-pass depletion electrofishing in the Kulukak River, July 2010. Model rankings and weights were based on delta AIC_c values.

Stratum	Habitat class	Model name	Parameters	AIC_c	$\triangle AIC_c$	Model weight
East Fork	EDZ	M_R	16	-5620.69	0	0.51
coho		$M_{R(effort)}$	17	-5619.02	1.66	0.22
		$M_{R(pass)}$	18	-5618.62	2.06	0.18
		$M_{R(pass+effort)}$	19	-5616.77	3.91	0.07
		$M_{R(pass*effort)}$	21	-5613.88	6.81	0.02
	Pool	$M_{R(pass)}$	6	-1115.30	0	0.35
		M_R	4	-1114.98	0.32	0.30
		$M_{R(pass+effort)}$	7	-1113.29	2.01	0.13
		$M_{R(effort)}$	5	-1113.16	2.14	0.12
		$M_{R(pass*effort)}$	8	-1112.58	2.72	0.09
	Riffle	$M_{R(pass)}$	7	-542.05	0	0.62
		$M_{R(pass+effort)}$	8	-540.98	1.08	0.36
		$M_{R(pass*effort)}$	11	-535.07	6.99	0.02
	Run	$M_{R(pass)}$	8	-1500.83	0	0.47
		$M_{R(pass+effort)}$	9	-1500.79	0.04	0.46
		$M_{R(pass*effort)}$	11	-1497.21	3.62	0.08

Appendix A2, continued.

Stratum	Habitat class	Model name	Parameters	AIC_c	$\triangle AIC_c$	Model weight
East Fork	EDZ	$M_{R(pass+effort)}$	20	-4290.40	0	1
sockeye	Pool	M_R	1	8.29	0	0.56
		$M_{R(effort)}$	2	9.89	1.59	0.25
		$M_{R(pass*effort)}$	3	12.73	4.44	0.06
		$M_{R(pass+effort)}$	3	12.73	4.44	0.06
		$M_{R(pass)}$	3	12.73	4.44	0.06
	Riffle	$M_{R(pass*effort)}$	3	-25.99	0	0.30
		$M_{R(pass+effort)}$	3	-25.99	0	0.30
		$M_{R(pass)}$	3	-25.99	0	0.30
		M_R	2	-22.84	3.16	0.06
		$M_{R(effort)}$	3	-21.39	4.61	0.03
	Run	$M_{R(pass*effort)}$	6	1.03	0	0.87
		$M_{R(pass+effort)}$	6	6.10	5.07	0.07
		$M_{R(pass)}$	5	6.45	5.42	0.06
West Fork	EDZ	$M_{R(effort)}$	13	-3463.01	0	0.50
coho		M_R	12	-3461.20	1.81	0.20
		$M_{R(pass+effort)}$	15	-3461.11	1.90	0.19

Appendix A2, continued.

Stratum	Habitat class	Model name	Parameters	AIC_c	$\triangle AIC_c$	Model weight
West Fork	EDZ	$M_{R(pass)}$	14	-3459.20	3.81	0.07
coho		$M_{R(pass*effort)}$	17	-3457.41	5.60	0.03
	Pool	$M_{R(pass)}$	11	-1296.68	0	0.61
		$M_{R(pass+effort)}$	12	-1295.50	1.17	0.34
		$M_{R(pass*effort)}$	14	-1291.46	5.22	0.05
	Riffle	$M_{R(pass+effort)}$	10	-618.99	0	0.36
		$M_{R(pass)}$	10	-618.66	0.33	0.31
		$M_{R(pass*effort)}$	12	-618.02	0.97	0.22
		$M_{R(effort)}$	10	-615.32	3.67	0.06
		M_R	9	-614.72	4.27	0.04
	Run	$M_{R(pass*effort)}$	16	-1017.12	0	1
West Fork	EDZ	M_R	10	-697.32	0	0.62
sockeye		$M_{R(effort)}$	11	-695.35	1.97	0.23
		$M_{R(pass)}$	12	-693.91	3.41	0.11
		$M_{R(pass+effort)}$	13	-691.90	5.42	0.04

Appendix A2, continued.

Stratum	Habitat class	Model name	Parameters	AIC_c	$\triangle AIC_c$	Model weight
West Fork	Pool	$M_{R(pass)}$	2	3.33	0	0.64
sockeye		$M_{R(pass*effort)}$	3	5.85	2.52	0.18
		$M_{R(pass+effort)}$	3	5.85	2.52	0.18
	Riffle	$M_{R(pass*effort)}$	8	-15.76	0	0.57
		$M_{R(pass)}$	6	-13.31	2.45	0.17
		$M_{R(effort)}$	6	-12.37	3.39	0.10
		M_R	5	-12.33	3.43	0.10
		$M_{R(pass+effort)}$	7	-11.20	4.57	0.06
	Run	$M_{R(pass+effort)}$	1	-57.33	0	1

Appendix A3. Plausible set of generalized linear models relating juvenile salmon density to six physical habitat variables: proportional area of cover by overhanging vegetation (OHV), large woody debris (LWD), and undercut banks (UCB), depth (m), velocity ($m \cdot s^{-1}$), and particle size index (see equation 2.3 in text for calculation of index values). Models were ranked in order of ascending ΔAIC_c; all models with $\Delta AIC_c < 8$ were included in the plausible model set.

		Model selection criteria				
Species	Plausible model name	AIC_c	*df*	ΔAIC_c	Akaike weight	Cumulative Akaike weight
Coho salmon	OHV + UCB + Velocity	108.1	5	0	0.83	0.83
	UCB	112.1	3	4.07	0.11	0.94
	OHV + LWD + UCB	114.0	5	5.92	0.04	0.98
	General	115.6	8	7.53	0.02	1.00
Sockeye salmon	PSI[†]	25.5	3	0.00	0.29	0.29
	Velocity[†]	25.5	3	0.03	0.28	0.57
	Intercept-only[†]	25.8	2	0.30	0.25	0.81
	OHV	28.4	3	2.89	0.07	0.88
	LWD	28.9	3	3.39	0.05	0.93
	Depth	29.7	3	4.21	0.03	0.97
	UCB	29.7	3	4.22	0.03	1.00

Appendix A4. Candidate regression model sets and AIC_c-averaged models of juvenile coho and sockeye salmon density and model parameter values (SEs in parentheses). Candidate models ($\Delta AIC_c < 8$) related density to six physical habitat variables: proportional area of cover by overhanging vegetation (OHV), large woody debris (LWD), and undercut banks (UCB), depth (m), velocity ($m \cdot s^{-1}$), and particle size index (see equation 2.3 for calculation of index values). Plausible model ($\Delta AIC_c < 8$) coefficients were averaged according to their Akaike weights to compute model coefficients (bottom row).

		Model parameter						
Species	Model name	Intercept	OHV	LWD	UCB	Depth	Velocity	PSI
Coho salmon	OHV+UCB +Velocity†	0.67	0.87	-	0.74	-	-2.44	-
		(0.12)	(0.76)	-	(0.99)	-	(0.99)	-
	UCB	0.40	-	-	0.33	-	-	-
		(0.09)	-	-	(0.93)	-	-	-
	OHV+LWD+UCB	0.03	0.82	0.48	0.68	-	-	-
		(0.19)	(0.81)	(1.00)	(0.94)	-	-	-
	General model	1.13	0.77	0.21	0.96	-1.45	-2.85	0.08
		(0.66)	(0.85)	(1.00)	(0.98)	(1.16)	(1.17)	(0.20)
	Velocity	1.88	-	-	-	-	-2.98	-
		(0.11)	-	-	-	-	(1.30)	-
	OHV	1.06	0.27	-	-	-	-	-
		(0.11)	(0.98)	-	-	-	-	-

Appendix A4, continued.

Species	Model name	Model parameter						
		Intercept	OHV	LWD	UCB	Depth	Velocity	PSI
Coho salmon	Depth + Velocity + PSI	2.79	-	-	-	-2.45	-2.96	-0.06
		(0.55)	-	-	-	(1.41)	(1.46)	(0.23)
	Intercept-only	0.347	-	-	-	-	-	-
		(0.08)	-	-	-	-	-	-
	Depth	2.06	-	-	-	-2.12	-	-
		(0.28)	-	-	-	(1.49)	-	-
	PSI	2.02	-	-	-	-	-	-0.25
		(0.60)	-	-	-	-	-	(0.22)
	LWD	1.41	-	0.0001	-	-	-	-
		(0.46)	-	(0.79)	-	-	-	-
	Averaged model	0.62	0.89	0.14	0.70	-1.45	-2.45	0.08
		(0.40)	(0.78)	(0.99)	(0.99)	(1.16)	(1.00)	(0.20)
Sockeye salmon	PSI†	1.65	-	-	-	-	-	-0.40
		(0.48)	-	-	-	-	-	(0.20)
	Velocity†	0.92	-	-	-	-	-1.67	-
		(0.19)	-	-	-	-	(0.81)	-

Appendix A4, continued.

Species	Model name	Model parameter						
		Intercept	OHV	LWD	UCB	Depth	Velocity	PSI
	Intercept-only†	0.74	-	-	-	-	-	-
		(0.19)	-	-	-	-	-	-
	OHV	0.91	-1.04	-	-	-	-	-
		(0.25)	(0.67)	-	-	-	-	-
	LWD	0.35	-	1.74	-	-	-	-
		(0.50)	-	(0.78)	-	-	-	-
	Depth	0.81	-	-	-	-0.52	-	-
		(0.55)	-	-	-	(3.69)	-	-
	UCB	0.72	-	-	0.15	-	-	-
		(0.28)	-	-	(1.00)	-	-	-
	Averaged model	1.04	0.74	0.97	0.02	-0.52	-1.67	-0.40
		(0.53)	(0.67)	(0.78)	(1.00)	(3.69)	(0.81)	(0.20)